NATIONAL ACADEMY OF SCIENCES.

Volume VIII.

SEVENTH MEMOIR.

WEST INDIAN MADREPORARIAN POLYPS.

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PART II.

WEST INDIAN MADREPORARIAN POLYPS.

By J. E. Duerden.

INTRODUCTION.

The insufficiency of our knowledge of the morphology of the soft parts of the Madreporarian corals has been commented upon by nearly all writers on the Anthozoa. Such a want at first seems remarkable, when we consider for how long and how fully the hard parts have been known, both to the zoologist and the palæontologist, and also the great abundance and wide distribution of living corals. When, however, the geographical limitations of the greater number of recent corals are taken into account, the difficulty of fully observing the polyps when alive, and more especially of preserving them and of carrying out their anatomical study, the deficiency can be in some measure understood. The investigations of a number of workers have already afforded an insight into the general structure of Madreporarian polyps, especially of the simple forms; but these are as yet insufficient to enable relationships of a broad systematic character to be established. Practically all that has been achieved along such lines is the demonstration that coral polyps are constructed on the same plan as the polyps of the principal group of the Actiniaria, the Hexactiniæ; in other words, that the mesenteries and other organs are arranged in a cyclical hexamerous manner.

Many writers have contributed descriptions and figures of living coral polyps; yet so few differences are determinable from external characters alone that Madreporarian morphology has been but little advanced thereby. For admirable reproductions of the external characters of living corals the works of Quoy and Gaimard (1830), Dana (1846), Klunzinger (1877), and the elaborate work of Saville Kent (1893), The Great Barrier Reef of Australia, should be consulted. In a recent contribution Prof. H. de Lacaze-Duthiers (1897) has presented a very full account of the corals met with in the Mediterranean, and the drawings of the living polyps are among the finest we possess. Undoubtedly the best illustrations of West Indian shallow-water corals, mainly limited, however, to the skeleton, are those accompanying the Report on the Florida Reefs, by Louis Agassiz (1880). In "The Stony Corals of the Porto Rican Waters," Mr. Vaughan has given thirty-eight photographic reproductions of the more familiar West Indian species (1901*a*), followed shortly by a more complete series from Prof. A. E. Verrill (1901).

Of the older writers on coral structure, Milne Edwards and Haime (1857), in their classic "Histoire Naturelle des Coralliaires," have given all that was then possible with the limited means of research available. It is only within the last two decades that any serious attempt has been made to advance our knowledge of the anatomical structure of Madreporarian polyps. The late Prof. H. N. Moseley, in 1882, proved that *Seriatopora* and *Pocillopora* are true Madreporaria,[a] and in his "Challenger" Report on the Deep-Sea Madreporaria made many other additions to the morphology of the group (1881).

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[a] Prof. A. E. Verrill (1869, p. 518), from descriptions and drawings of *Pocillopora*, had come to the same conclusions as early as 1867.

In the papers "Die Gattung *Cladocora*" (1881) and "Korallenstudien" (1886, 1891), Prof. A. R. von Heider has described in detail the anatomy and the relationships of the polyps to the corallum in two species of *Cladocora*, and *Astroides calycularis*, *Dendrophyllia ramea*, and *Madracis pharensis*. The work of von Heider is especially noteworthy on account of his contention that the skeleton of corals is derived from an actual calcification of the ectodermal cells or calicoblasts.

Dr. G. H. Fowler, in a series of five papers, "The Anatomy of the Madreporaria," appearing in the Quarterly Journal of Microscopical Science, from 1885 to 1890, has described in greater or less detail the soft parts of a larger number of corals than any other student of the group, and has brought together many important details of coral structure. In the introduction to his first paper Fowler gives a review of the little that was then known of the anatomy of the Madreporaria.

Prof. G. C. Bourne, in two papers, also published in the Quarterly Journal of Microscopical Science (1887), describes at some length the anatomy of the corals, *Fungia*, *Mussa*, and *Euphyllia*. In 1893 Bourne gave a detailed description of the postembryonic development of *Fungia*, founded on material collected by Prof. A. C. Haddon, while in 1899 he published a masterly account of the nature and origin of the skeleton in the Anthozoa, dealing particularly with the Madreporarian skeleton and the calicoblastic layer. Bourne has also contributed the article "Anthozoa" to Prof. Ray Lankester's Treatise on Zoology (1900), wherein he gives a clear account of many of the structural details of the Madreporaria.

W. L. Sclater, in 1886, contributed an anatomical description of *Stephanotrochus moseleyanus*, and J. Stanley Gardiner (1900) has given a detailed account of the "Anatomy of a supposed new species of *Cœnopsammia* from Lifu;" Miss Edith M. Pratt (1900) has described the anatomy of *Neohelia porcellana* (Moseley).

Prof. G. von Koch, in a large series of papers, extending from 1877 to the present day, has probably done more than any other worker toward elucidating the problems of Madreporarian morphology, on the correct lines of embryology and the relations of the hard and soft parts as revealed by microscopic sections.

Prof. H. de Lacaze-Duthiers, in 1872–73, made two valuable embryological contributions, "Développement des Coralliaires," and records the results of the first attempts to rear coral larvæ to the skeleton-bearing stage, while his figure of the anatomical relations of the soft and hard parts of *Astroides calycularis* has been copied into many of the text-books of zoology. Two recent publications of Lacaze-Duthiers (1894, 1897) contain descriptions of a number of early stages in the development of several coral species.

Prof. H. V. Wilson (1888) has carried out a very complete study of the embryology and larval stages of *Manicina areolata*, as far as the stage at which the skeleton was about to appear; Prof. A. C. Haddon (1890) has also published notes on the newly hatched larva of *Euphyllia*.

In all probability the polyps of not more than fifty species of corals have been anatomically studied, and then often incompletely, owing to the insufficiency of well-preserved material. It must be acknowledged, that in so far as the results throw light upon the important question of the natural relations of the various groups of corals, they are disappointing, especially when the great amount of labor involved in conducting the investigations is taken into account. Similar anatomical researches carried out on the allied group of the Actiniaria, by workers such as the brothers Hertwig, Haddon, McMurrich, Carlgren, and many others, have resulted in placing our knowledge of these forms upon a fairly satisfactory morphological basis. No doubt it will yet be possible to accomplish the same for the Madreporaria, as the polyps of more species, especially reef-builders, become fully known.

A residence in Jamaica, in the neighborhood of coral reefs, has afforded me the opportunity of studying, within the past two or three years, the West Indian shallow-water corals in their living condition, and of preserving them for subsequent examination. And in this connection I desire to record my appreciation of the liberal action of the Board of Governors of the Institute of Jamaica in enabling me to carry out such researches, purely scientific in their nature.

In the shallow waters of Kingston Harbor, Jamaica, occur free colonies of the following species of corals: *Porites divaricata*, *Manicina areolata*, *Siderastræa radians*, *Cladocora arbuscula*, *Solenastræa hyades*, and *Oculina diffusa*. Any of these can be easily kept in aquaria in a laboratory, for weeks or months at a time, by simply renewing the fresh-water lost by evaporation. The functional activity of numerous symbiotic unicellular algæ (*Zooxanthellæ*), present in the endodermal tissues of each species, is sufficient to maintain the water in a fit state of aeration and purity.

For typical reef-building corals, such as species of *Madrepora*, *Porites*, *Mæandrina*, and *Orbicella*, the most convenient collecting spots are among the small group of coral islands, termed "Cays," beyond Kingston Harbor and Port Royal. From the reefs surrounding these over twenty further species are to be obtained, and other localities around the island yield practically the same forms; also at certain places in Kingston Harbor reef-building corals occur at accessible depths. As would be expected from the uniformity of climatic conditions, the Jamaican corals are such as are generally distributed throughout the entire West Indian region.[a]

All the species here studied have been examined in their living condition, and usually from an abundance of material. In most cases the colonies were kept alive for some time within the laboratory, so that the varying aspects of the polyps during expansion and retraction could be observed. Much indeed of the character of the polyps is to be obtained in this way, which is impossible from retracted preserved polyps.

Most of the material for anatomical study was preserved with the polyps narcotized in a partly expanded condition, in order to render possible a better study of the relationships of the various organs and of the skeleton. When killed otherwise the polyps shrink deeply within the calice, the stomodæum becomes flattened by resting upon the central portions of the skeleton, and the arrangement of the mesenteries, etc., can be ascertained only with difficulty. For narcotization I have employed either magnesium sulphate or menthol, and both methods give satisfactory results. The use of menthol as a narcotic is very simple. It is merely necessary to sprinkle a few crystals on the surface of the water, when the reagent becomes slowly absorbed and gradually anæsthetizes the polyps; pure formol is then added to the water in sufficient proportions to make a 5 per cent. solution, and the polyps usually undergo no further change. The polyps may retract and shrink slightly if the process of narcotization is incomplete, but never to the same extent as if preserved directly. Though very desirable for museum purposes, a polyp expanded to its utmost offers no advantages for anatomical and histological study. The tissues in this condition are so attenuated as not to permit of the characteristics, especially those of the musculature, being determined with the same facility as in only moderately expanded examples. Usually the polyps expand fully only at night, or when placed in the shade, and the process of narcotization requires several hours. At night it was generally found convenient to add slowly the crystals of magnesium sulphate or menthol and allow them to act upon the polyps until morning, when the addition of formol brought about no retraction.

The proper preservation of the soft tissues of the Madreporaria has always been a matter of some difficulty, but the employment of formol is found to be fairly satisfactory. I have adopted it as a 5 per cent. solution in either fresh or sea water. Especially is the reagent serviceable on account of its penetrative powers; in all cases the preservation of the internal tissues was equal to that of the external, the ciliation being recognizable in most instances. There is an element of uncertainty, however, as to how long the histology will remain perfect in the formol solution alone. In some instances material which had remained in the original preservative fluid for five or six months has been found satisfactory for microscopic study, but in others a slight maceration has taken place. In this latter case the details of the anatomy and coarser histology can be still made out, but the more minute histology is imperfect. The possibility of maceration holds especially for forms like *Porites*, which exude a large amount of mucus on preservation. To guard against such risks, I have found it necessary to transfer the specimens, shortly after preservation in formol, through the different grades of alcohol up to 90 per cent. Where material intended for histological research has to be kept for some time this is undoubtedly desirable. On the other hand, for museum purposes expanded coral polyps, anemones, and medusæ have been kept in a solution of formol for several years without any obvious deterioration.

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[a] For lists of these see the papers by Pourtalès, Agassiz, Quelch, Duchassaing and Michelotti, Verrill, Gregory, and Vaughan, referred to in the Bibliography. The figures and references to corals in the old natural histories of Jamaica by Sir Hans Sloane (1707) and Dr. Patrick Browne (1756) are well worthy of notice, as also those of Lesueur (1820).

An aqueous solution of corrosive sublimate or corrosive acetic has also been employed with great advantage, in that it fixes the tissues so completely that on decalcification there is little or no alteration in the relationships of the different organs. It is much superior to formol or alcohol in this respect. Before commencing the decalcification of material which has been in alcohol or formol for some time, I have often found it advantageous to pass it through a solution of corrosive sublimate.

Decalcification has generally been performed in a weak solution of hydrochloric or nitric acid, after the material has been thoroughly hardened. The acid is added drop by drop to a fragment of the coral still in the preservative fluid in sufficient quantities to maintain a slight effervescence. From one to two days are required for the decalcification of small pieces of porous corals, such as *Madrepora* and *Porites*, whereas the decalcification of dense coralla, like those of *Siderastræa* and *Oculina*, occupies three or four days. Where it has been desirable to carry out the decalcification with special care, as in investigations of the calicoblast layer and skeletal matrix, very weak solutions of acetic and chromic acids have been employed, and then the process requires a much longer period. When, as is usually the case, perforating algal matter occurs within the skeleton, it is advisable to remove this from time to time, so as to keep a fresh calcareous surface exposed.

If decalcification of properly fixed material be slowly carried out, there is little or no disturbance of the primary relationships of the soft parts. After a few attempts, I concluded that nothing was to be gained by making preparations of the hard and soft parts *in situ*, such as are obtained by embedding fragments of a colony in canada balsam and then grinding down to microscopic thinness. All the figures of the sections are, so far as concerns the relationships of the soft and hard parts, actual reproductions of camera lucida drawings. The irregularity in outline of many of the septal invaginations can be understood when one considers how generally the septa are provided with spines or granules.

Much of the work has been carried out while in Jamaica, and the remainder during the academical year 1899–1900, in Professor Brooks's biological laboratory at the Johns Hopkins University.[a] My thanks are due to Prof. W. K. Brooks for many valuable suggestions and much kindly interest during my stay in Baltimore; also to Prof. A. C. Haddon, of the Royal College of Science, Ireland, and Prof. G. B. Howes, of the Royal College of Science, London, for much assistance and encouragement from time to time during the progress of the work. I am indebted to Rear Admiral (then Commodore) H. N. Henderson for generously affording me facilities for collecting in the waters around Port Royal and the Cays beyond. Mr. T. Wayland Vaughan, of the United States Geological Survey, has assisted me in the specific determinations. In his recent account of the fossil corals from Curaçao (1901), and also of the stony corals of the Porto Rican waters, Mr. Vaughan (1901*a*) has dealt with the difficult subject of the synonymy of West Indian corals.

The paper is divided into two parts. The first is devoted to a more general description of the external characters and morphology of coral polyps, so far as the material available will permit, and the second to a description of the external characters and internal anatomy of certain representative species. To the former a few notes on larvæ and postlarval development are added, which, although incomplete, assist in an understanding of the significance of many of the adult features. In a large measure, also, I have carried out comparisons with the better-known Actiniaria. The polyps of the two groups are so closely alike that a knowledge of the characters in the one often assists in throwing light upon conditions in the other. In the second or systematic part, I have ventured to indicate some of the broader lines of relationships among the Madreporaria, suggested by the new facts obtained, and have attempted for the first time generic diagnoses in terms of the polyp. It will be understood that where generic characteristics are given they have reference only to the representatives here studied. The isolation under which the

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[a] Since the presentation of the paper the studies have been continued, and results of some importance obtained, which amplify certain of those here given, particularly those on growth by gemmation and fissiparity. They are referred to in foot-notes on various pages.

work has been carried out, away from collections of all but West Indian corals, has rendered impossible a comparison with other species.

A complete knowledge of any coral form can be obtained only from a full description of both the polypal and skeletal parts, such as has been carried out in a few cases by Fowler, von Heider, Bourne, and Gardiner. But in the present instance it has been deemed advisable to confine the studies wholly to the soft parts; for some time such will remain the most pressing need among workers of the group.

The main object of the work has been to determine, from an examination of as many coral forms as possible, the principal facts of morphology within the group, and the illustrations are in the main limited to these.[a]

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[a] The following is the list of species studied. The terminology and orthography adopted is mainly that of Milne and Edwards and Haime (1857). The recent papers of Vaughan (1901, 1901a) and Verrill (1901) have shown that this is in great need of revision. I have added the names suggested by these authors where they differ from those here employed. In the descriptive part of the work the usual references and synonyms of the species are omitted, as these are sufficiently noticed in the papers mentioned, and also in that of Gregory (1895).

Madrepora muricata Linnæus—forma *cervicornis* (Lam.); forma *prolifera* (Lam.); forma *palmata* (Lam.)=*Isopora muricata* (Linn.) [Vaughan]=*Acropora muricata* (Linn.) [Verrill].
Porites astræoides Lamarck=*Porites astreoides* Lam. [Vaughan]=*Porites astreoides* Lam. [Verrill].
Porites clavaria Lamarck=*Porites porites* (Pallas) forma *clavaria* Lam. [Vaughan]=*Porites polymorpha* Link [Verrill].
Porites furcata Lamarck=*Porites porites* (Pallas) forma *furcata* Lam. [Vaughan].
Porites divaricata Lesueur=*Porites porites* (Pallas) forma *divaricata* Le Sueur [Vaughan].
Astrangia solitaria Lesueur.
Phyllangia americana Milne Edwards & Haime.
Cladocora arbuscula (Lesueur).
Orbicella annularis (Ellis & Solander)=*Orbicella acropora* (Linn.) [Vaughan].
Orbicella radiata (Ellis & Solander)=*Orbicella cavernosa* (Linn.) [Verrill].
Orbicella cavernosa (Linnæus).
Solenastræa hyades (Dana).
Stephanocœnia intersepta (Esper).
Favia fragum (Esper).
Dichocœnia stokesi Milne Edwards & Haime.
Isophyllia dipsacea Dana.
Manicina areolata (Linnæus)=*Mæandra areolata* (Linn.) [Verrill].
Colpophyllia gyrosa (Ellis & Solander)=*Manicina gyrosa* (Ell. & Sol.) [Verrill].
Mæandrina labyrinthica (Ellis & Solander)=*Platygyra labyrinthica* (Le Sueur) [Vaughan]=*Mæandra cerebrum* (Ell. & Sol.) [Verrill].
Diploria labyrinthiformis (Linnæus)=*Mæandra labyrinthiformis* (Linn.) [Verrill].
Pectinia mæandrites (Linnæus)=*Mæandrina mæandrites* (Linn.) [Vaughan].
Oculina diffusa Lamarck.
Siderastræa radians (Pallas).
Siderastræa siderea (Ellis & Solander).
Agaricia fragilis Dana.
Agaricia agaricites (Linnæus).

PART I.

GENERAL MORPHOLOGY.

In any living coral, be it a simple or colonial form, the soft polyp above can be readily distinguished from the hard, calcareous skeleton below. The latter is generally cup shaped, and serves as a support and protection to the former. Structurally the polyp is very simple, and is either distinct or united with others. While alive it is variously colored, and assumes very different appearances according as it is fully expanded or retracted within its calice. When expanded it presents two distinct regions—a smooth column, generally cylindrical in outline, and terminated distally by a more or less flattened oral disk. In the center of the latter is the slit-like mouth, while toward its periphery are one or more cycles of simple or knobbed tentacles. Sometimes the polyps, instead of being distinct and independent, retain but partial individuality, and give rise to complicated discal, tentacular, and columnar systems.

Upon decalcification the nearly colorless basal or aboral region of the polyp becomes exposed. This is generally cylindrical or conical, and very complex in detail, being deeply grooved obliquely or vertically, and otherwise invaginated in correspondence with the skeletal projections; terminally it may be truncated or tapering.

The interior of the polyp is hollow, but much subdivided by two series of vertical partitions, arranged in cycles. The members of one series—the mesenteries—hang from the body wall, their free edge provided with a filamentous organ, except above, where some unite with the stomodæum depending from the margin of the oral aperture; the other partitions—the septal invaginations—are wedge-shaped inturnings of the basal wall, which are occupied by the skeleton, and are arranged so as to alternate with the mesenteries. Invaginations of the basal wall may also occur centrally, when they are usually connected with the septal inturnings. The mesenteries cease before the aboral termination of the polyp is reached, while the septal invaginations are best developed below, and distally never extend the whole length of the expanded polyp.

Microscopically the body wall is constituted throughout of three distinct layers, very different in character. The outer comprises various glandular, protective, and sensory elements; the middle is a nearly homogeneous, jelly-like substance; while the inner is mainly constituted of glandular and muscle cells, and is often loaded with unicellular algæ, the so-called zooxanthellæ.

On any colony new polyps, originating either as buds or by division of some other polyp, are to be found in various stages of growth. Within the mesenterial mesogloea of the mature polyps may occur groups of sexual cells, and within the polypal cavity may be free larvæ undergoing the early phases of development. Such are the broad features characteristic of Madreporarian polyps, and these will now be described in greater detail.

COLUMN WALL.

As comparatively few coral polyps have been described from their appearance in the fully expanded condition, the descriptive term *column* has been but little employed in Madreporarian literature, though of universal recognition in works on the Actiniæ for the corresponding region. When coral polyps are fully expanded their columnar character is usually very obvious, but in the retracted condition it is not so evident, and is further confused because one portion of the column may be within the calice and another outside; also, owing to the colonial habit of most species, the line of separation of the column wall of one polyp from another is not always readily determinable.

The retention of the word column becomes absolutely necessary for a correct appreciation of the morphological relationships of the corresponding regions in the various types of coral growth. The region admits of a very precise definition, and, except in a few instances, of distinct limitations on the living or preserved colony. In the Actiniaria the column includes the whole of the polypal wall between the basal disk and the oral disk, the latter limited peripherally by the outermost cycle of tentacles. It is also usually distinguishable from the rest of the polyp by structural differences, especially in the stronger development of the musculature distally.

Embryological results indicate, as was first established by Professor von Koch (1882), that in Madreporarian corals the basal disk of the larva or young polyp first gives rise to the skeleton, and, however complicated the latter ultimately becomes, the tissues lining it directly (skeletotrophic or skeletogenic) are morphologically those of the base. It follows from this that the line at which the skeleton-producing tissues pass into the superficial tissues is the boundary between the true basal disk and column (Pl. XIX, fig. 137). The latter will thus include all the superficial part of the polypal wall between this boundary and the outermost row of tentacles, and nowhere takes any part in the formation of the skeleton. Column wall and oral disk will thus practically correspond with "oral body wall," and basal disk with "aboral body wall," as these terms are employed by Fowler, Ogilvie (1896, p. 107), and others. By body wall or polypal wall I understand the whole or any part of the wall of the polyp—base, column, and oral disk.

In simple polyps, and at the margin of colonial polyps, the boundary between the basal wall and the column wall is entire, and is indicated by a marked histological difference; but in colonial polyps, elsewhere than at the margin, interruptions exist which permit of free communication between the internal cavities of the various polyps constituting a colony (Pl. XII, fig. 87). Mesenteries are attached for some distance along the basal skeletotrophic wall, and then pass up the column wall, and in the case of the complete members are continued across the disk and down the stomodæum.

The column wall, as above defined, is easily distinguished in the simple polyps of *Astrangia*, and *Phyllangia* (Pl. V, fig. 46); but in colonies, where the asexually produced polyps remain connected with one another, the limitation of the wall of the individual polyp is not always readily determinable externally. Many colonial genera, including such as *Orbicella*, *Siderastræa*, and *Porites*, display a smooth polygonal groove which represents the external line of demarcation of the polyps. The superficial tissues are in partial continuity with the skeletotrophic tissues along these grooves, either directly or through the intermediation of the mesenteries, and the groove is therefore incapable of elevation above the skeleton, even on full expansion (Pl. IX, fig. 67).

The two or three polyps, which as a rule constitute the sub-colonies of *Cladocora*, afford interesting stages in the separation of the body wall of polyps primarily united (Pl. VI, fig. 48). Usually each polyp presents a free portion along its lower margin, where the ectoderm of the column can be seen to pass into that of the base, while the remainder is united with the termination of the wall of the other polyps, the line of union being indicated by a groove. As the polyps increase in size this line of connection diminishes in extent, the communication between the cavity of one polyp and of the other ceases, and ultimately the polyps separate, though usually not before each has given rise to one or more buds.

The polyps of *Oculina* (Pl. XXII, fig. 149) are spirally arranged, and as a rule widely separated; in the older regions of colonies the limitations of the individual columns are not readily seen, but can be easily made out in young colonies, and at the growing regions of others. Where the boundary is indicated the pericalicular mesenteries extend as far as the limitations of each polyp; but where the polyps have become widely separated, the mesenterial prolongations cease before the limitations of the polyps are reached, and then no actual boundary between one and another persists.

In fissiparous genera like *Favia* and *Isophyllia*, in which one or a few oral apertures may occur on a single disk, a single wall is common to each disk, but is separable from those adjacent, as in the cases just described. The fissiparous conditions met with in these genera become more complex in *Manicina*, *Mæandrina*, *Pectinia*, and *Colpophyllia*. Here the column wall, like the disk and the tentacular zone, is common to a large number of oral apertures, but along the thecal ridges (collines) a longitudinal groove occurs, separating the column of two adjacent systems. A further condition occurs in *Agaricia*. New polyps seem to arise by fission, and each possesses its own system of tentacles; there is, however, no precise boundary line or groove between the column wall of adjacent polyps. A prominent thecal ridge imperfectly marks off one polyp from another (Pl. XXIV, fig. 162), but no external indication is afforded that the column wall becomes adherent to the corallum along its apex.

Madrepora is another genus in which no external demarcation occurs between the superficial tissues of the various polyps making up a colony; it is impossible to say where the column wall of one polyp ends, and that of another begins. As shown on Pl. I, fig. 1*a*, representing a fully expanded apical polyp, the free cylindrical region, which should undoubtedly be regarded as a column, passes directly into the superficial covering of the colony; but on this there is no groove limiting the column of one polyp from those surrounding it.

In simple corals, and around the periphery of colonies, the lower or proximal extremity of the column wall is closely adherent to the corallum, and upon decalcification its uninterrupted passage into the basal skeletotrophic tissues can be followed, the histological structure of the two differing greatly. The upper distal margin of the column continues to grow upward, the lower extremity keeping pace with it, and the skeleton below is thus left exposed. Usually foreign growths, particularly Nullipores,[a] in time settle upon the exposed part of the corallum; or it may be attacked by destructive agents,[b] such as boring sponges or mollusks, or by tubiculous worms.

At the actual boundary of the column wall and basal disk a thin deposit of calcareous matter usually takes place, which in coral terminology is known as the "epitheca." This generally shows signs of stratification or wrinkling, the thickened lines representing periods when the upward growth of the polypal margin was not proceeding rapidly, and consequently more calcareous formation took place. In the early stages of *Manicina areolata*, the column wall practically envelops the whole of the corallum, and all stages in its growth upward, according as the colony enlarges, can be obtained. In the skeleton the epitheca is clearly seen as a thin calcareous layer resting upon the edges of the costæ, its upper margin indicating both the proximal extremity of the column wall and the commencement of the skeletotrophic tissues when the colony was alive. The region at which the epitheca is formed is clearly seen on Pl. XIX, fig. 137, representing a section through a young polyp of *Manicina*, and also on Pl. XIV.

RANDPLATTE OR EDGE-ZONE, CŒNOSARC, CŒNENCHYME.

The term "Randplatte" was originated by von Heider (1881, p. 4), when describing the external features of the Mediterranean *Cladocora*, to include the continuation beyond the crown of tentacles of the soft parts of the polyp over the border of the calice. It has since been extensively employed in Madreporarian literature by Fowler, Bourne, and Miss Ogilvie, the latter of whom introduced "Edge-zone" as its English equivalent (1896, p. 108). Referring to the name, G. von Koch (1886, p. 342), in a foot-note, draws attention to the fact that the region alluded to is no structure "sui generis," and therefore possesses no independent morphological significance.

In expanded coral polyps there is really no demand for such a descriptive term, as in this state the column wall stretches vertically, in undivided continuity, from the margin of the tentacular crown to its line of union with the wall of the surrounding polyps, and, except for a stronger development of the endodermal musculature above, the histological structure of the wall is the same throughout. Most of the mesenteries also extend the whole length of the column. Where,

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[a] In *Astrangia solitaria* the incrusting Nullipores sometimes grow upward with such rapidity as to cover the whole of the external surface of the corallites, displacing the pericalicular part of the polyp. They may even extend over the thecal edge so as to sensibly diminish the aperture through which the polyp protrudes.

however, the calicinal wall extends peripherally far upward within the cavity of the polyp, then upon retraction of the latter the upper region of the column becomes drawn within the calice, but the lower region, still with the mesenteries attached to it, remains outside. It is to this external area of the column wall, often sharply marked off in retracted polyps, that the term "edge-zone" is usually restricted. As a result of the same upgrowth of the calicinal wall, the cœlenteron likewise becomes separated into calicinal and pericalicinal or perithecal portions, each partitioned into chambers by the mesenteries, and less so by the septal and costæ (Pl. VII, fig. 54).

Among corals like *Porites* and *Siderastræa*, in which the calicinal wall is common to adjacent polyps, and the septa are but little or not at all exsert, there can possibly be no extrathecal, or rather pericalicinal or perithecal, continuations of the tissues, and no edge-zone.

By "edge-zone" Dr. Ogilvie (p. 108) understands "that the mesenteries of the interseptal loculi are continued into the intercostal loculi," thus giving a more precise meaning to the term than was done by von Heider. Among all the forms here studied, which are provided with a perithecal continuation of the gastric cavity into intercostal loculi, *Madrepora* is the only one in which the mesenteries also are not prolonged perithecally. In this genus the superficial covering of the colony is continuous with the column wall of the polyp, and, as shown on Pl. I, fig 2, the cœlenteron is directly continuous over the edge of the theca with the superficial canals, but there is never any trace of external mesenteries. In the expanded polyp the mesenteries are seen to pass from the extruded column wall directly into the calice, and the column wall below, unsupported by mesenteries, rests directly upon the skeletal echinulations.

The precise definition given to the edge-zone affords Miss Ogilvie the opportunity of accomplishing the same for the somewhat loosely employed term "Cœnosarc." By this the authoress (p. 108), following Bourne (1888, p. 26), signifies "an extrathecal part into which the mesenteries do not continue." Cœnosarc will, of course, consist of two distinct tissues: the skeletal covering proper (base), and the superficial covering to the colony (column wall), the two separated more or less by a continuation of the gastro-cœlomic cavity.[a] By universal acceptation, "Cœnenchyme" is the calcareous deposit originating from the cœnosarc, and this is only laid down by the skeletotrophic layer, the inner of the two external tissues. According to the definition of cœnosarc and cœnenchyme just given, *Madrepora* alone, among all the forms available for study, is characterized by these structures; that is to say, the only genus in which the perithecal walls of the polyp are without mesenteries (Pl. I).

One of the most illustrative examples in this connection is *Oculina*. In all the definitions of the genus one of the characteristics given is the presence of a solid cœnenchyme. Yet throughout young colonies, and in the growing regions of others, the mesenteries are prolonged perithecally, so as to extend as far as the spiral groove of separation of the superficial tissues of the different polyps, and the corresponding grooves on the skeleton are determinable throughout. It is only in the older regions of large colonies that the mesenteries do not extend the whole length of the column wall, and the skeletal surface then becomes perfectly smooth, with an absence of grooves or costal ridges. Under such circumstances it becomes impossible to draw any sharp line between edge-zone or column wall and cœnosarc. The latter is merely the extracalicular region of the polyp into which the mesenteries are not prolonged.

Bourne (p. 26) states that "a common cœnosarc is due to nothing more than a persistent connection between the 'Randplatten' of adjacent polyps, and that the two structures are homologous." This undoubtedly holds for some forms, e. g., *Galaxea*, but the first portion of the definition can scarcely be regarded as applicable to cases like *Madrepora*, where, by defini-

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[a] At the points where the cœnosarc rests upon the costal ridges or echinulations the two coverings are combined, and the skeleton is here overlaid only by the superficial ectoderm, the mesoglœa, and the calicoblastic ectoderm (Pls. I, II). The perithecal gastro-cœlomic cavity then becomes represented by canals, often reticular in character. Fowler (1888, p. 7, Pl. XXXII, figs. 2, 3) shows that in *Amphihelia ramea* the direct adherence of the polypal wall to the skeleton may become very broad, the canals being, as it were, pushed apart from one another and greatly narrowed.

Of the canals in *Cœnopsammia* Gardiner (1900, p. 361) observes: "The cœnosarcal canals in fact are simply extrathecal portions of the cœlentera of the different polyps, which serve to connect their intrathecal or gastrovascular portions."

tion, there is no Randplatte, and one can hardly employ the term homologous in connection with structures which are merely continuations of one another.

Cœnosarc then, no more than Randplatte, is a polypal structure "sui generis;" the two are merely special regions of the column wall and underlying skeletotrophic layer, in the latter case provided with mesenterial continuations, and in the other devoid of them. Cœnenchyme likewise is inseparable from the portion of the thecal wall laid down by the extrathecal layer of the morphological basal disk, under whatever name it may be known. The terms have merely a topographical, not a morphological, significance.[a] In the following pages column wall will generally include the whole of the external body wall, from the line at which it passes below into the skeletogenic tissues to the outer margin of the tentacular zone above.

Fowler, in his studies of various species of corals, has given much attention to the relationship of the peripheral part of the column wall to the skeleton, particularly to the manner in which it may be said to be supported. At first it appeared that in species without cœnenchyme the column wall was supported upon only the perithecal continuations of the mesenteries ("peripheral lamellæ"), while in species with cœnenchyme the wall was directly supported upon only echinulations of the skeleton. Pl. VII, fig. 54, and Pl. XIX, fig. 132, will serve as examples of the former, and Pl. I, figs. 2–6, taken from *Madrepora*, are instances of the latter method. Later, however, Fowler found that no such rule could be maintained; that the two methods of support—mesenterial and echinulate—might co-exist in the same form, e. g., *Madracis*, *Amphihelia*.

Where mesenterial continuations occur, the perithecal portion of the polypal cavity exists as a series of simple vertical canals; but where mesenteries are absent, and the column wall rests directly upon skeletal ridges or echinulations (*Madrepora*), the cavity is usually broken up into a complicated system of canals.

FORM AND ANATOMY.

Externally the column wall of coral polyps presents few structural modifications compared with the same region in the Actiniaria. There is an entire absence of the simple or complicated columnar outgrowths often displayed in the latter group, and nothing comparable with a capitulum or cycle of acrorhagi has been observed, the column always passing uninterruptedly into the tentacles. Practically the only external distinction in this direction concerns the surface of the column, whether smooth or verrucose. The latter condition is brought about by the presence of teeth or spines on the edges of the costæ and septa. Where these occur the polypal walls on retraction come to rest upon them, and the areas over the projections become slightly raised above the general surface, assuming a warty appearance; and even on fullest expansion, when free from the corallum, the tubercle-like character rarely entirely disappears. Sometimes the verrucæ are indicated by a slight color distinction, and often give a coarse appearance to the polyps. Where the edges of the costæ and septa are smooth, or only finely toothed, the surface of the outer polypal tissues is likewise smooth. Histologically the verrucæ present no differences from the rest of the column wall, except that their constituent layers are generally thinner. They are thus to be distinguished from the verrucæ of Actiniæ, which are slightly modified evaginations of the wall, or more often take the form of vertical rows of suckers, with a strongly marked histological modification. The verrucæ in corals are characteristics dependent upon the form of the skeleton, rather than a structural differentiation of the soft tissues.

Corresponding with the costæ and septa, the verrucæ are arranged in vertical intermesenterial rows, larger and smaller rows often alternating, in agreement with the large and small skeletal partitions. This is readily seen in species of *Orbicella*, *Favia*, and *Manicina*, while in *Mæandrina* all the rows are equal. The verrucæ in any single row are somewhat irregular in size and height

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[a] The study of the *Cœnopsammia* from Lifu has lead Gardiner (1900, p. 361) to define cœnosarc in such a way as to make it much more embracive than would either Bourne or Miss Ogilvie. Thus: "*The Cœnosarc is that part of the polyps in a colony which lies outside but not above (i. e. in expanded state) the thecæ of the several corallites.* The 'Randplatte' of von Heider and von Koch, the 'edge-zone' of Miss Ogilvie, is then that part of the cœnosarc which lies over the free portions of the corallites."

in a form like *Isophyllia*, where the septal and costal spines are very variable in the amount of development. The external grooves which separate the verrucal ridges correspond with the line of attachment of the internal mesenteries, and are always smooth.

Apparently there are no permanent apertures in the column wall of Madreporarian polyps, such as zoophytologists are familiar with in the "Cinclides" of the Sagartids among the Actiniaria. Through these latter the thread-like "Aeontia," loaded with nematocysts, are extruded when the polyp is irritated. The majority of coral polyps, however, have the power of extruding prolongations of the mesenteries bearing coiled mesenterial filaments along their edge (p. 475), but these can evidently perforate any portion of the superficial tissues, the disk equally with the column wall. Careful examination of the body wall, before the filaments are extruded, fails to reveal any apertures, and their irregular distribution, sometimes over nearly the whole external surface of the polyp, would suggest that the apertures are merely temporary and may be produced at any point. On Pl. VIII, fig. 64, is represented a section through a portion of the column of a polyp of *Orbicella annularis* through which the filamental part of a mesentery is extruded. No histological modification whatever can be made out in the wall itself; the aperture is a mere interruption of the layers for the passage of the mesentery and its filament. Upon the polyps settling down after irritation the filaments are slowly indrawn, and ultimately no external indications remain of the apertures through which they protruded. In some cases the openings have been observed to remain distinct for a short time after the indrawal was completed, but the injury, if such it can be regarded, was soon completely healed.

On full expansion of the polyp the column may extend for some distance above the corallum, and is either cylindrical, oval, or irregular in form. Proximally, where it is fixed to the skeleton, it assumes the outline of the individual corallites, and hence may be circular, polygonal, or irregular. In species of *Siderastræa* and *Agaricia* the column appears never to be raised much above the general surface of the corallum, and in forms like *Mæandrina*, with incomplete polypal separation, the column on both sides rises for many millimeters as a vertical expansion, with a deep valley separating one polypal row from another.

The form and position assumed by the intercalicular portion of the column wall upon retraction of the polyps varies greatly. In most cases the upper region of the column becomes folded inwardly over the edge of the theca, while in some it is merely drawn downward. In the former condition it either comes to lie inclined downward against the oblique septa (*Manicina*, *Mæandrina*, etc.), or, by the action of the endodermal circular muscle, it extends horizontally, terminating in a circular margin which nearly meets at the center, and thus almost covers the disk below (Pl. X, fig. 74). In *Madrepora* the wall becomes merely drawn within the calice without any overfolding (Pl. I, fig. 2); in *Siderastræa* and *Agaricia* the column and disk are simply depressed, and come to rest upon the skeleton, leaving the tentacles and mouth wholly exposed (Pl. XXII, fig. 150).

Variations in the position assumed by the column wall on retraction of the polyps are sometimes observable even in the same species. Thus the wall in *Porites clavaria* may be slightly folded over the disk, or, as in *Siderastræa*, it may merely come to rest upon the corallar surface, the tentacles and disk remaining exposed (Pl. IV, figs. 34 and 35).

Among the skeletonless *Actiniæ* the column wall is usually of some thickness, so as to give more or less rigidity to the body of polyp, but in the Madreporaria, where support is afforded by the skeleton, the polypal wall is nearly always a thin, delicate, often transparent structure. In both groups the thickness of the wall is mainly determined by that of the middle layer—the mesoglœa, as both the ectodermal and endodermal epithelia vary comparatively little. By contrast with that of most anemones the mesoglœa in the column wall of corals is, as a rule, little more than a mere separating lamella between the inner and outer layers, except along the line of attachment of the mesenteries, where it becomes somewhat thickened in a triangular manner.

The thickness of the column wall is also partly dependent upon the state of expansion or retraction of the polyp. On full distention all three layers become greatly attenuated, the ectodermal and endodermal cells largely diminished in height, and the mesoglœa scarcely distinguishable as a separate layer. The walls are then much more nearly transparent than in the retracted state. In sections the column wall varies from 0.1 millimeter across in *Isophyllia dipsacea* to 0.023 millimeter in *Agaricia fragilis*.

The three polypal layers will now be described in more detail.

ECTODERM.

The ectoderm of the column of Madreporarian polyps is a regular, often ciliated, columnar epithelium, constituted mainly of unicellular gland cells, supporting cells, and scattered nematocyst-bearing cells; muscle and nerve fibrils are rarely if ever recognizable in sections. The nuclei of most of the cells are arranged at nearly the same height in the layer, and in sections of moderate thickness give rise to a very definite nuclear band or zone. The nuclei thus regularly distributed are mainly those of the long narrow supporting cells; the nuclei of the gland cells and nematoblasts are less restricted and occur nearer the mesoglœa.

The ciliation of the column wall is by no means so pronounced as in the case of the stomodæal ectoderm and mesenterial filaments, and few observations have been made to determine its general distribution in the living polyp, or the conditions of its activity. Traces of cilia sometimes remain in preserved material, and the effects of its activity are often noticeable on the living polyp. When light particles of foreign matter are dropped on the large discal area of a coral like *Manicina*, they are seen to be slowly transferred to the margin of the disk, but, instead of merely dropping over, they are dragged in a definite manner along the column, and only discarded, as it were, when they reach its lower termination. When similar particles are dropped on other living polyps they are likewise set in movement in a more or less definite manner, but no such action could be distinguished on the living tissues of *Favia fragum*.

The glandular cells of the columnar ectoderm are mainly oval shaped toward the periphery of the layer, and narrow internally; the base is generally fibrillar and rests upon the mesoglœa (fig. 8). The contents are nearly homogeneous and rarely stain, usually appearing quite clear; at other times they are finely granular and stain more readily. The cells are mucus secreting, and their different behavior toward reagents probably indicates different stages in the development of the cell and its secretions. In addition to the clear mucus cells, long, narrow gland cells occur of which the contents are coarsely granular, and these take up most stains with great avidity. They seem to be different in character from the other gland cells, and, as a rule, are but sparsely represented.

In most cases the gland cells occupy the greater proportion of the layer, so much so that in tangential sections through the outer portions of the ectoderm the cells form a close polygonal network, the interstices being occupied by a few supporting cells (Pl. X, figs. 76–78). Quantities of clear, colorless mucus are given out by most corals upon disturbance, as, for instance, when a fragment from a large colony is broken off; also upon preservation in a limited quantity of sea water sufficient mucus may be extruded to give a jelly-like consistency to the liquid. The presence of the mucus upon the surface of a colony often interferes with the proper preservation of the polyps. This is especially the case with *Porites*, where both the ectoderm and endoderm are highly glandular (Pl. IV).

As a rule the column wall of coral polyps contains a few scattered nematocysts, which, however, are never aggregated into distinct batteries such as occur on the tentacles. They are always small, of two or three kinds, and are easily distinguished from the long, narrow, tentacular form, or the large oval variety more characteristic of the endoderm.

In the genera *Isophyllia* and *Mæandrina*, and to a less degree in certain others, the superficial tissues in the living condition appear dense and almost opaque. Histological examination reveals that the mesoglœa of the column wall in these is a little thicker than usual, but the chief cause of the opacity evidently lies in the contents of the ectodermal cells. This is illustrated by the genus *Orbicella* (Pl. VIII, fig. 65). Clear mucus-secreting cells occur with comparative rarity, and the chief cellular constituents of the layer are long supporting cells, the nuclei of which are elongated and arranged in a very regular zone, so closely that in places they appear to exert a mutual pressure upon one another. The deeper parts of the layer are characterized by the presence of patches of finely granular pigment matter, arranged closely or somewhat distant from one another. In the areas of greatest concentration the granules extend almost to the periphery of the ectoderm, but they are mainly internal to the nuclear zone. Probably they are to be regarded as of the nature of pigment granules, and are to be distinguished from the granules of glandular cells. They are manifestly the chief cause of the general opacity of the body wall in many fissiparous species. (See also, *Isophyllia*, Pl. XVII, fig. 122.)

MESOGLŒA.

The mesoglœa[a] of coral polyps has generally been described as a perfectly structureless layer, without any of the migrant connective-tissue cells, such as are characteristic of the mesoglœa of the greater number of Actinian polyps. The homogeneous condition is found in many of the species here described, especially where the polyps are small, but in others it becomes somewhat more complex. The layer stains feebly, or not at all, and when perfectly homogeneous and transparent may be indistinguishable from the clear field of the microscope.

In large polyps, such as *Isophyllia dipsacea*, and also in *Mæandrina*, the mesoglœa is rather thick, and minute connective-tissue cells occur sparsely throughout. In sections the cells are circular or oval in shape, with a central nucleus, and minute prolongations extend in all directions; many of these reach one or other of the surfaces of the layer, and there come into contact with the ectodermal or endodermal cells. In some instances the processes extend right across from one layer to the other, but are mostly disposed in an irregular stellate manner. Their close connection with the ectoderm and endoderm would seem to indicate their origin from one or both layers, except in the mesenterial mesoglœa, where obviously they can be derived only from the endoderm.

The mesoglœa is usually of uniform character and consistency throughout any polyp, but a slight difference is revealed in preparations of *Isophyllia dipsacea*, which have been stained with borax carmine and methyl blue. The layer is colored a bright blue, but narrow tube-like portions, which scarcely take up any coloring matter, stretch across the layer, or in other sections appear as small, light-colored disks; with hæmatoxylin it remains unstained, and exhibits no such differentiation.

The ectodermal and endodermal surfaces of the mesoglœa are mostly even, but in some regions, especially on the face of a mesentery which bears the longitudinal musculature, the surface becomes folded, or may even form complicated branching plaitings, so as to afford an increased area for the muscular fibrils (Pl. XVIII, fig. 130). The endodermal surface in the uppermost region of the column may also be deeply folded for the same purpose (Pl. XVII, fig. 121). In no case, however, has the musculature been found to become actually embedded within the mesoglœa of the column, such as occurs among anemones where a strong mesoglœal sphincter is formed (*Sagartidæ*).

As the mesoglœa is practically alike in structure throughout the tissues of any polyp, it will be unnecessary again to refer to it in detail in describing the individual organs. Along the line of attachment of the mesenteries to the skeletotrophic tissues, and less frequently elsewhere, peculiar mesoglœal processes occur which seem to serve as a means of attachment of the polypal tissues to the skeleton (Pl. XIII, fig. 95). They are fully referred to on page 481.

ENDODERM AND SPHINCTER MUSCLE.

Gland cells, both in the clear and granular condition, are the main constituents of the endoderm. Supporting cells are less numerous than in the ectoderm, while the musculature is

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[a] In a preliminary note, "On the Anatomy of a supposed New Species of *Cœnopsammia* from Lifu," Mr. Stanley Gardiner proposes the name "skeletoglœa" for the structureless lamella or jelly of the Actinozoa, instead of a "makeshift term," such a "mesoglœa." The introduction of this new term would undoubtedly lead to great confusion if employed in the literature of skeleton-producing polyps, while such has never been the case with Bourne's term, now universally adopted. "Skeletoglœa" would have served aptly for the jelly-like, homogeneous matrix in which the skeleton is laid down (p. 483). In his fuller paper (1900, p. 358), Gardiner prefers to use the term "structureless membrane" or "basement membrane."

better developed, and symbiotic algæ or zooxanthellæ are nearly always present. The ciliation is feeble, and rarely determinable in preserved material.

The endodermal layer is of much the same character throughout the polyp, whether in the column wall, tentacles, disk, skeletotrophic tissues, or forming the mesenterial epithelium. It may vary slightly in thickness in different regions, and in the greater or less preponderance of glandular cells, while in nearly all the species a remarkable modification of the skeletotrophic endoderm takes place in the lower regions of the polyp. The layer here becomes much thicker and loses its distinctly cellular character, appearing finely reticular. So greatly thickened does the endoderm become that it often nearly obliterates the gastro-cœlomic cavity in the most proximal region of the polyp. The chief constituents—nuclei, cytoplasm, zooxanthellæ, and in some cases granular gland cells—are mostly accumulated in a narrow peripheral zone, the deeper portion being vacuolated or bearing only fine granules (Pl. X, figs. 73 and 75).

Zooxanthellæ occur in large numbers within the endoderm cells of all the species studied, with the exception of *Phyllangia americana* and *Astrangia solitaria*. They are usually distributed throughout the polyp, but are more numerous in the exposed tissues (column wall, disk, tentacles) than in the endoderm of the mesenteries and skeletotrophic tissues: they even occur within the internal canals of the perforate genera *Madrepora* and *Porites*, but are never found free or detached within the polypal cavities except in larvæ. As described on page 437, the organisms are the principal cause of the coloration of many coral polyps. Large oval nematocysts occur in the endoderm of *Porites* and *Madrepora*, but are absent from most other genera. Their numbers and distinctive form in the genera mentioned are such as to leave no doubt that they are actually formed in the endoderm, not free examples injested from the ectoderm.

The circular endodermal musculature of the column wall appears to be always present in coral polyps, as in Actinian polyps, though varying much in the degree of its development; as a rule it is stronger at the uppermost region of the column wall than below. Sometimes the fibrils are scarcely to be found anywhere, while in other species they become strongly developed distally, and give rise to a typical diffuse sphincter muscle, such as is characteristic of many Actiniæ (e.g., *Corynactis*). This is seen in species of *Orbicella*, especially in the large *O. cavernosa*, but also in the smaller *O. annularis* (Pl. VIII, fig. 65). Here, in retracted polyps, the mesoglœa is thrown into deep folds for additional support to the musculature. The muscle fibers lining the hollows or grooves never become separated from the superficial layer, as happens in Actinians where the muscle is truly mesoglœal. In other species of corals the mesoglœa forms only very slight folds, while again it may be perfectly smooth, indicating a very weak muscular development.

The sphincter muscle is more strongly developed in *Isophyllia dipsacea* than in any other species here studied. In vertical sections of the uppermost region of the column wall the mesoglœa displays one or more special thickenings which are much plaited, the whole lined with muscle fibers (Pl. XVII, fig. 121). The structure very closely recalls the type of sphincter described by Haddon (1898, p. 432) as occurring in the Actinian *Macrodactyla*, and there termed a "restricted" sphincter muscle. It represents a stage of muscular development more complex than that described as "diffuse." The plaitings appear on several axes of greater or less complexity; while in the "circumscribed" sphincter muscle of Actinian anatomy they are restricted to a single axis. The amount of development of the sphincter muscle is manifestly dependent upon the size of the polyp, the polyps of *Isophyllia* and *Orbicella* being among the largest studied.

The action of the circular sphincter muscle is to bring about the overfolding of the distal region of the column wall upon retraction of the polyps. This occurs in nearly all corals, and, as already observed, it results that the column wall almost completely hides the disk and tentacles, leaving a small central opening over the oral aperture. Circular constrictions may occur in the column wall without any retraction of the disk, in this case the action of the columnar musculature is probably the same as before, but the retractor muscles of the mesenteries have not come into play and drawn downward the oral region of the polyp.

G. H. Fowler (1888a, p. 12) was the first to record the presence of an undoubted sphincter muscle in the Madreporaria, having found the mesoglœal plaitings strongly developed in *Sphenotrochus rubescens.* Gardiner (1900, p. 363) also describes a strong circular sphincter muscle in *Cœnopsammia.*

The sphincter, sometimes known as "Rötteken's muscle," is usually strongly developed in Actiniaria, where it assumes very varied forms, and becomes of great importance for taxonomic purposes. Actinian polyps in general are capable of retraction to a greater degree than are coral polyps, but where no sphincter is present the disk and tentacles always remain exposed. There is no doubt that the actual outline assumed by the mesoglœal plaitings supporting the fibrils, and giving its character to the muscle, is largely dependent upon the amount of retraction and extension of the polyp, but still sufficient constancy remains to justify the importance attached to the muscle for diagnostic purposes.

A few observations upon the general expansion and retraction of coral polyps may be here given.

EXPANSION AND RETRACTION OF POLYPS.

Only the more superficial tissues of coral polyps—column wall, disk, tentacles, and upper part of the mesenteries—are capable of expansion and retraction, the change being brought about mainly by the action of the musculature of these regions, with an accompanying entrance or expulsion of water from the polypal cavity. The skeletotrophic tissues are destitute of muscle fibers, and throughout remain adherent to the corallum, perhaps held in position by the peculiar wedge-shaped or conical structures originating from the desmocytes (p. 482); hence they take no part in the varying aspects of the polyp.

Polypal expansion proceeds slowly by the imbibition of sea water into the internal cavity, and the consequent distension of the body wall. The musculature being relaxed, entrance of the water is effected through the oral aperture, probably as a result of the activity of the strongly developed stomodæal cilia. On retraction of the muscles, and subsequent diminution in size of the polypal cavity, the water is largely expelled, also through the mouth. In a colony where the cœlentera of all the polyps are in communication with one another, there seems no reason why water should not be abstracted from one region to another, so that the polyps in one part may be expanded and those in another retracted. The polyps of one area of a colony are often in a different state of expansion from those of another. If an expanded colony be suddenly lifted out of the water, flaccidity of the tissues almost immediately results, due to the loss of water, and the latter can be actually observed flowing from the internal cavity. On irritation of a single polyp in a fully distended colony the polyp readily retracts, and those around more slowly, the water issuing through the mouth as a distinct stream.

Polypal retraction is brought about by the united action of the musculature of the mesenteries, column wall, disk, and tentacles, the first mentioned being probably the most important. The longitudinal retractor muscles are always more or less well developed on one face of each mesentery, the mesoglœa being often folded to give increased area. By the contraction of these muscles the distal region of the polyp is drawn downward; at the same time the contraction of the circular endodermal musculature of the column wall aids in the shrinkage, and the same is to be said of the circular musculature of the disk.

From the comparative development and arrangement of the muscle fibrils throughout coral polyps, it is manifest that retraction is entirely dependent upon muscular contraction, while expansion is mainly due to the relaxation of the muscles, followed by the entrance of water.

The external appearance of corals varies greatly, according as the polyps are expanded or retracted, and it is only from a full knowledge of both conditions that a clear understanding of the relationships of the polyps to the corallum can be obtained. On complete retraction the superficial tissues come to lie more or less closely upon the upper part of the corallum, always separated, of course, from direct contact by the adhering skeletogenic tissues. In strongly retracted examples of most species the costæ and septa are seen through the polypal walls and stand out prominently, and the tissues over them are much thinner than the portions of the wall which occupy the intervening depressions. Where the edges of the septa or costæ are sharply spinous, as in *Isophyllia*, the points appear as if perforating the tissues; but it may be doubted whether this ever occurs naturally, as sections reveal only a great thinning of the layers. Polyps of *Madrepora*, *Cladocora*, and *Astrangia*, having a tubular calice, are able to withdraw their upper parts so deeply within the latter as to render the disk and tentacles almost invisible. Most members of the Astræidæ also partly withdraw themselves within the calice, and at the same time, by the contraction of the sphincter muscle, the capitular region of the column wall is drawn, iris-like, over the disk and tentacles, leaving but a small central aperture through which the mouth and central part of the disk can usually be seen. In *Manicina* and *Colpophyllia* the columnar musculature is weakly developed, and when retracted the capitular region is partly drawn downwardly and inwardly, covering the tentacles, but leaving the middle discal area exposed. In *Madrepora*, *Porites*, *Siderastræa*, and *Agaricia* the column wall is very rarely overfolded; on retraction the disk and tentacles are merely drawn downward, coming to rest upon the corallum, and the tentacles, disk, and mouth remain exposed.

During full expansion the upper part of the polyp is elevated some distance beyond the corallum, and the perithecal portion of the gastro-cœlomic cavity becomes swollen.[a] The column wall, instead of being folded horizontally or downward over the theca, now stretches nearly vertically from its line of union with the other polyps and skeleton as far as the tentacular zone. This alteration of form can be easily understood in the case of distinct polyps, but not so readily in species where the polyps are incompletely separated.

Manicina is a good example of the latter in which to compare the different appearances of polyps on expansion and retraction. In the latter condition the meandering disk rests upon the skeletal projections on the floor of the calice, and the upper part of the columnar expansion lies obliquely upon the upper edge of the septa, then folds over the margin of the theca, and is continued downward over the outside of the theca for a distance varying in different examples. On full distension the disk is raised several millimeters above the skeleton, becoming much broader and flattened, or even convex; the tentacles are arranged in a marginal zone, either overhanging or partly involved in the discal tissues. The column wall is elevated vertically, its lower margin being the line along which the superficial tissues pass into the tissues lining the skeleton, and this for the time being constitutes the lower fixed termination of the column.

Mæandrina and *Colpophyllia* are somewhat more complicated. The living colony during the day usually exhibits a meandering system of columnar ridges and discal valleys; the column extends about half way within the calice, folded and slightly swollen as it terminates, and more or less hiding the rows of tentacles. Full distension completely reverses the relationship of the disk and column wall. The former now becomes raised from its depressed condition along the floor of the calice until it is some millimeters wholly above the corallum, and convex in vertical section; the adjacent column walls are also raised until they become nearly vertical, and are either pressing against one another laterally, or separated only by a deep, narrow groove, at the bottom of which lies the line of connection of the column wall to the skeleton. The former discal valleys are now the ridges, and the thecal ridges the bottom of the valleys.[b]

A few observations have been made with regard to the external conditions which seem to determine the state of expansion or retraction of coral polyps. As a general rule the polyps are not expanded to their full degree during the day, either on the reef or in the laboratory; but the process begins immediately after sunset, and full expansion is maintained for the greater part of the night. Thus on bringing into the laboratory, in the course of the morning, a collection of specimens, they usually remain retracted for the rest of the day, but after sunset (6.30 to 7.15 p. m. in Jamaica) the polyps begin to expand until they attain their full dimensions. The body cavity is greatly distended with water, and the column wall and disk become raised some

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[a] Where the pericalicular continuation of the gastro-cœlomic cavity has become broken up into irregular canals, as in *Madrepora*, the amount of distension is small; but even in this genus a marked difference is seen in the cœnosarc, according as the canals are fully charged or nearly empty.

[b] Verrill (1863, p. 38), from an examination of alcoholic specimens of *Mæandrina*, *Manicina*, and *Favia*, came to the conclusion that the polypal disk does not rise even level with the summit of the corallum. Also naturalists familiar with the Bahama and Bermuda corals have informed me that they have never seen many of the fissiparous species (e. g., *Isophyllia*) in an expanded state.

distance above the corallum, while the tentacles are erect or overhanging. The colonies remain in this state nearly all night, unaffected by any artificial light employed in observing them; even when the strong light from a condensing lens rests upon a polyp for some time there is no response. In the morning the polyps are again found retracted.

If injured too much in the process of collecting, as when a portion of a colony is with difficulty broken off a large mass, the polyps of most corals are unable to recover sufficiently to expand at night. The best specimens for laboratory study are the colonies found lying free on the sea floor, for these can be removed without much disturbance to the living animals.

On the reefs, *Mæandrina*, *Colpophyllia*, and *Orbicella* are found partly expanded during the day, only the tips of the tentacles and part of the disk being visible; *Manicina* will sometimes protrude its tentacles, but *Isophyllia* rarely so. On the other hand, *Madrepora* and *Porites* are usually fully expanded; colonies of both species are often met with *in situ* on which, by means of a water glass, all the polyps are seen protruding to their full extent.

The corals found in very shallow water in Kingston Harbor are mostly retracted during the day; but if collected with care, and placed in shallow glass vessels exposed to the full rays of the sun, such species as *Manicina areolata*, *Porites furcata*, *Siderastræa radians*, *Cladocora arbuscula*, and *Oculina diffusa* will expand fully. Further, when in the laboratory these species have been kept shaded from the sun during the early part of the morning and are then brought into its direct rays, they soon begin to expand, and remain so for some time. Also, on bringing corals which during the whole day have been kept in a cool, shaded place into the rays of the setting sun they nearly always respond to the change and expand fully. It may be that in such experiments it is not the strong light but rather the slight increase of temperature of the water which exercises some stimulating influence on the polyps.

The general experience is that if colonies are placed in shaded spots during the day the polyps respond to the change, and expand to a greater or less degree, but if exposed to full light they remain retracted.

Much difference is experienced in the readiness with which various coral species expand. In the laboratory *Agaricia* seems to open less freely than others; *Cladocora* and *Oculina* are among the readiest to open out. In some instances the polyps of the latter remained fully distended for two or three days together without ever retracting.

It may, therefore, be taken as a general rule that coral polyps expand to their full degree during the night, but that under artificial conditions they may respond to an increase of light and temperature. The whole question of their response to external conditions is full of interest, but can be solved only by a long series of observations and experiments.

That night expansion is not restricted to tropical corals may be gathered from the observations of Gosse (1860, p. 312) on *Caryophyllia Smithii*. This British species was also found to expand most freely at night.

Many sea anemones exhibit the same phenomena as coral polyps, though not to the same degree. Colonies of the Zoanthid *Palythoa* are found in plenty on the reefs; during the day the polyps are mostly in the retracted state, and in the laboratory night is always found to be the most suitable time for examining them in the fully distended condition.

In the course of his examination of the coral reefs of Funafuti, Rotuma, and Fiji, Mr. Stanley Gardiner (1898) found much the same results as regards the time of expansion of coral polyps; *Euphyllia*, *Symphyllia*, and *Mussa* were the only corals observed by Gardiner to be fully expanded in the daytime. He further states, as is also the case in West Indian waters, that only during the night is the tow net able to collect in any quantity the minute larvæ, eggs, and other small organisms which probably constitute the food of coral polyps. During the day such pelagic forms evidently sink to the deeper waters, reappearing nearer the surface at night, and becoming most abundant in the early morning.

It may be that night expansion and day retraction of the coral polyps are in some way connected with this distribution of their food, and it is not unlikely that the phenomenon may be associated with the strong local sea breezes which usually disturb tropical waters during the day, and produce a cloudiness some distance around the shores. At night and early morning, the breezes having subsided, the waters are quieter and more favorable to the activities of delicate sessile animals.

Perhaps the activity of the unicellular commensal algæ, present in such great numbers in the endodermal tissue of nearly all species, may be associated with the changes. But fully expanded, more transparent tissues in the daytime, would manifestly be most favorable for the functional activity of their chloroplasts.

TENTACLES.

The tentacles of Madreporarian polyps exhibit a certain diversity of form and arrangement, though not to the same degree as the corresponding organs in the Actiniaria. They are mostly disposed around the margin of the oral disk, in two or more entacmæous, alternating cycles. In *Madrepora* and *Porites*, however, they appear to constitute only a single cycle. In living polyps the tentacles can usually be seen to correspond in position with the internal mesenterial chambers of which they are the external prolongations, and further to conform in position, and, as a rule, in number, with the internal skeletal septa. In nearly all cases they correspond exactly with the number of internal mesenterial chambers, both entocœlic and exocœlic. Tentacles arising from the entocœlic mesenterial chambers may be known as *entotentacles*, and those from exocœlic chambers as *exotentacles*. Where present the latter always constitute the outermost cycle, and all the inner cycles consist of entotentacles. In *Siderastræa* the exotentacles differ in form from the entocœlic members (Pl. XXII, fig. 151), while in *Agaricia*, and the fully developed apical polyps of *Madrepora*, exocœlic tentacles are wanting. Gardiner (1900, p. 365) also found the tentacles to be entocœlic only in *Cœnopsammia*.

In all coral polyps so far described only one tentacle arises from each mesenterial chamber. The number of tentacles therefore represents the actual number of mesenteries present, and, in general, the number of septa also. None of the species examined shows the stichodactylinous condition so prevalent among tropical Actiniæ.[a]

During extension the tentacles are usually elongated, broad below and narrow above, the walls thin and somewhat transparent. Most of the species studied are characterized by a white, opaque, knob-like apex, more or less distinct, and constituting a battery of nematocysts. The tentacular stems of coral polyps are rarely smooth throughout, but exhibit round, oval, or irregular opaque thickened patches, which, like the apical knob, are aggregations of nematoblasts. These are elevated a little from the general surface, but rarely show any spiral or other regular disposition. Such restrictions of the tentacular nematoblasts are very exceptional among Actinians, and in this group the knobbed condition is also unusual (*Corynactis*, *Corallimorphus*).

With the exception of *Siderastræa radians* and *S. siderea* the tentacles of all the species here described are simple, while in the genus mentioned the entotentacles become bifurcated toward their free extremity, but the exotentacles remain simple.

In the living polyp the tentacles assume varied positions. During retraction they are usually withdrawn within the calice, and completely hidden by the overfolding column wall; but in some genera, *Siderastræa* and *Agaricia*, they remain exposed under all conditions of retraction or expansion of the polyps. In *Porites* and other forms the tentacles may occasionally remain exposed on retraction of the polyps, though more usually hidden under the retracted column wall. Upon expansion of the polyp the organs stand erect or overhang, even to such an extent as to nearly hide the column wall; and on the same polyp different cycles may sometimes assume different attitudes, as where the inner cycle is erect and the outer overhangs. The tentacles of corals rarely display much independent motion when fully extended, compared with the activity exhibited by the long tentacles of anemones. The tentacles of *Cladocora* and *Siderastræa*, and probably others, possess considerable adhesive power, more especially at the apex; the distal part of the stem may also fold round any small object. When small annelids are placed

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[a] The term is applied to polyps (e. g., *Corynactis*, *Discosoma*) in which the tentacles are arranged in radial rows, so that more than one tentacle communicates with a single mesenterial chamber. The character serves to distinguish the tribe *Stichodactylinæ* from other Actiniaria in which only one tentacle communicates with a mesenterial interspace.

upon living colonies of *Siderastræa* the tentacles of the expanded polyps at once close upon them and prevent their escape.

The detailed arrangement of the tentacles presents many differences in the various species studied. As seen externally, the twelve tentacles of *Madrepora* and *Porites* (Pls. I and IV) admit of no proper distinction into an inner and an outer series, though varying somewhat in size, and may therefore be described as acyclic or monocyclic; the apical polyps of the former genus bear only a simple cycle of six equal tentacles. Although forming only one cycle, the twelve tentacles in both genera represent two orders, constituted of six entotentacles and six alternating exotentacles. The tentacles of such genera as *Orbicella*, *Solenastræa*, *Oculina*, *Cladocora*, and *Astrangia*, whose asexual method of reproduction is by gemmation, usually exhibit a regular hexameral multicyclic arrangement, with the formula 6, 6, 12, 24, etc. Very often the first and second orders are arranged so as to form only one inner cycle of twelve members, with which the twelve members of the second cycle alternate; the third cycle of twenty-four alternates with both these, and so on, according to the number of cycles developed. Where only twenty-four tentacles are present they usually appear as an inner and an outer cycle.

Very often the hexameral sequence of the tentacles is not complete, especially in *Cladocora* and *Astrangia*. The total number of tentacles in mature polyps of *Cladocora arbuscula* varies from thirty-two to thirty-six, whereas the complete hexameral plan would require forty-eight as the next number after twenty-four has been reached. In describing below the development of the later tentacles of polyps, it is found that the organs do not arise a complete cycle at a time, but in simple or double pairs on each side of the median axis, and in many species a tentacular cycle once commenced is not always completed before the polyp attains its full size and growth ceases. In such a case it is clear that any intermediate number of tentacles between the commencement of a cycle and its completion may be present.

Whenever an entocœlic tentacle appears, a corresponding exocœlic member usually arises, either simultaneously or shortly after, so that the number of exotentacles comprising the outer cycle is always equal to the sum of the entotentacles of all the inner cycles. Hence in endeavoring to establish the cyclic scheme of any hexameral polyp, in which the number of tentacles may be intermediate between twenty-four and forty-eight, or forty-eight and ninety-six, incompletion must be looked for in the two outermost cycles, not in the outermost only. A polyp of *Cladocora* with thirty-two tentacles bears the cyclic formula 6, 6, 4, 16; one with thirty-six tentacles the formula 6, 6, 6, 18; with forty tentacles 6, 6, 8, 20, where the numbers 16, 18, and 20 represent the exotentacles. The exocœlic cycle thus increases by the same amount as the outermost entocœlic cycle. The order of appearance of the tentacles demonstrates that it is impossible to establish hexameral completion for all the cycles until the outermost is reached, and then relegate any omissions to this, as is usually attempted. Any omission due to hexameral incompletion affects both the exocœlic and the last entocœlic cycles.

The members of any tentacular cycle are nearly always alike in size, but the tentacles usually show a diminution in length in passing from the inner to the outer series, a condition expressed by the term entacmæous. The organs in *Madrepora* and *Porites* are exceptional in that they vary in size in a very definite manner in the same cycle, while *Orbicella radiata* offers a marked exception to the entacmæous order. The polyps of this species do not readily expand their tentacles, and hence are not always favorable for observation. When fully extended the different tentacular cycles are found to be widely apart, and the twelve members comprising the first cycle are much smaller than those of the next, and even less than the tentacles of the outermost cycle. The tentacular plan of a polyp of *O. radiata*, with three hexamerous cycles, is represented on the next page.

Usually the different cycles which constitute the crown of tentacles are closely arranged in a narrow marginal zone, so that basally the members of one cycle partly embrace those of the next. *O. radiata*, just mentioned, is again exceptional in that a wide discal interspace separates one cycle from the next, the tentacular crown being unusually broad, encroaching upon the peristome. The same feature is also characteristic of the polyps of *Siderastræa* and *Agaricia*;

the cycles are widely apart, and each individual tentacle is distant from the others. In these two genera the tentaculiferous area comprises nearly the whole of the exposed polypal surface (p. 427).

In polyps whose asexual method of reproduction is by fission, the hexameral plan, characteristic of larval polyps, and of adult polyps whose reproduction is by gemmation, is lost after fission is established, and even the cyclic arrangement becomes obscure. In *Favia*, *Isophyllia*, and *Manicina* individual tentacles belonging to several cycles can be made out, but not with any regularity all round. The tentacles in the young polyps are found to be arranged hexamerously, but this is altogether lost on mature colonies. Where fission is never or rarely completed, as in *Mæandrina* and *Pectinia*, the tentacles are arranged in meandering systems, and only two rows are developed, an inner entocœlic series and an outer alternating exocœlic series.

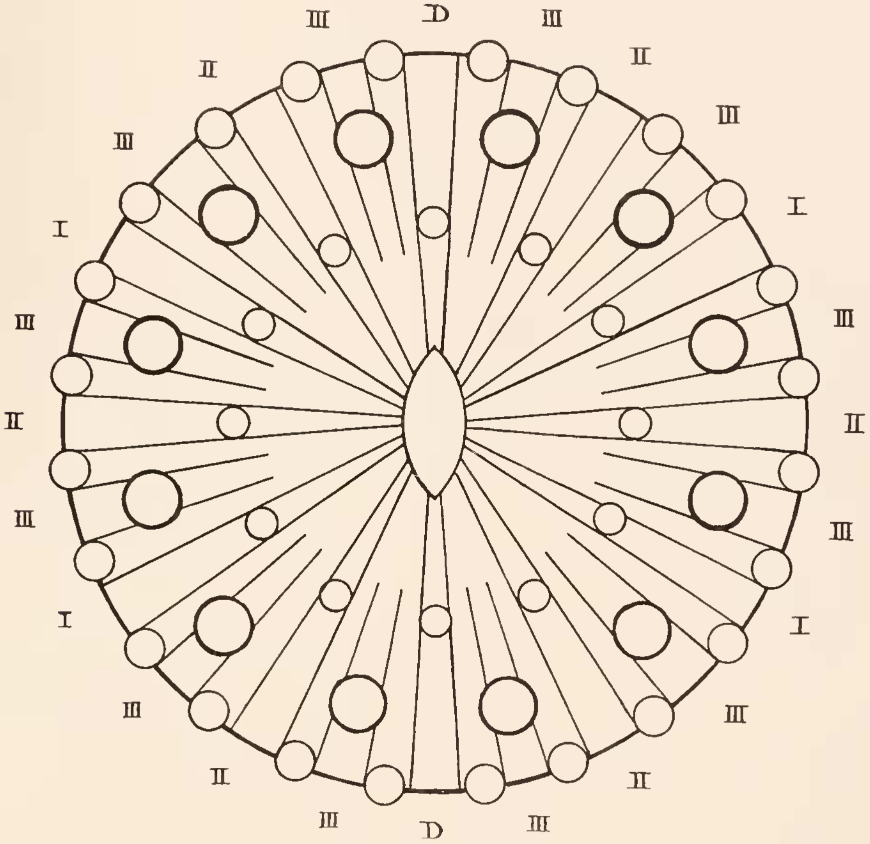

FIG. 1.

Tentacular plan of a polyp of *Orbicella radiata*. The Roman numerals indicate the orders of mesenteries; D, the directives. The innermost cycle of tentacles comprises twelve members, which are the smallest of the series. They arise from the entocœles of the first and second orders of mesenteries, which constitute the first cycle of twelve pairs of complete mesenteries. The second, middle cycle consists of twelve alternating tentacles, which are the largest represented. They are outgrowths of the entocœles of the third order of mesenteries, which form the actual second mesenterial cycle. The third or outermost cycle is formed of twenty-four tentacles, which alternate with the members of the two previous cycles, and arise from exocœlic chambers. The species is exceptional in that the members of the innermost cycle are the smallest of the series, and also in the wide distance apart of the cycles.

When the polyps retract, the tentacles do the same, and become greatly shortened. In addition, many species of corals exhibit the curious phenomenon of complete introversion of the tentacles, even during full expansion of the polyps, as well as on retraction. Both phases are clearly illustrated in the tentacles of *Porites* (figs. 30, 33, 40). At times the polyps in this genus will be expanded to their full degree, without any display of tentacles; twelve small, more opaque, circular areas, sometimes showing a central aperture, are all the external indications of their presence, while the local increased opacity indicates that they have become invaginated within the cœlenteric cavity. At other times one or more individual tentacles of a polyp may be protruded, while the rest are inturned. The process of introversion and subsequent extension has been actually observed on the expanded polyp. The movements of the tentacular walls, inwardly or outwardly, take place so slowly that they can be readily followed, the process somewhat resembling that seen when a glove finger is indrawn and afterwards pushed out. The alternations may be continued for some time. Likewise on retraction of the polyps the tentacles of *Porites* are, as a rule, introverted, instead of remaining merely exposed or covered by the column wall; and on preserved colonies very small apertures can be detected with a lens at the place of introversion. In longitudinal sections through such polyps the apical knob of the tentacle is deepest within the gastro-cœlomic cavity, and is directed outwardly, while with regard to the walls themselves, the ectoderm is internal and the endoderm external, a reversal of the ordinary condition. These conditions are clearly shown in fig. 40, representing a vertical section through a polyp of *Porites astræoides*. No overfolding of the column wall has taken place on retraction, so that the tentacles communicate directly with the surface of the colony. Three introverted tentacles (*t*) are present; the one to the left is divided radially, so that the section includes its aperture of communication with the exterior, while the two to the right are tangential sections, and therefore do not display the external opening. Again, in fig. 30, representing a transverse section through the stomodæal region of the same species, seven introverted tentacles are seen in section, almost completely occupying the mesenterial chambers, and exhibiting a reversal of the ordinary relations of ectoderm and endoderm. In other polyps sectionized a variable number of introverted tentacles has been met with. The apex of the introverted tentacle may extend as far inwardly as below the inner termination of the stomodæum, so that accompanying the introversion very little diminution in the length of the stem has taken place.

Among the living expanded polyps of *Madrepora* also complete tentacular introversion is often observed, in both apical and radial polyps. In the former six slight opacities around the margin of the transparent disk remain to indicate the tentacular area; later, the tentacles may be observed to protrude, either all together or successively.

During the retracted condition of the fissiparous genera *Favia*, *Manicina*, *Mæandrina*, and *Isophyllia* it is sometimes impossible to discover any tentacles externally. When sections are made, however, the organs are found to be introverted, occupying both the entocœlic and exocœlic mesenterial spaces.

In addition to actual introversion, in which all parts of the tentacles are still determinable, a condition is often presented in which the stem wholly disappears, becoming a part, as it were, of the discal wall.

Retracted tentacles of *Siderastræa* and *Agaricia*, for example, are usually represented by only a slight tubercular elevation of the disk, which is the knob or swollen apex, while the stems have wholly disappeared in the disk (Pl. XXIII, figs. 154, 155, and Pl. XXIV, fig. 163). In microscopic sections the former are displayed as mere ectodermal thickenings, charged with nematocysts, and no differentiated can be found whereby the tentacular stem can be distinguished from the discal wall.

Among the fully expanded polyps of *Orbicella annularis* the two cycles of short tentacles often wholly disappear. Here, again, it appears as if the tentacular tissues were not introverted, but rather have become involved in the greatly expanded margin of the disk; slightly raised, triangular areas, representing the apical swellings, are all that can be observed of the organs. On full extension of the adult polyps of *Manicina areolata* the tentacles likewise may be wholly wanting, their walls having become part of the expanded disk. Thicker, more opaque discal spots, which are the only evidence of their former presence, represent the nematocyst-bearing capitulum. In the young polyp of *Manicina* displayed in section on Pl. XIX, fig. 137, the tentacle appears only as a thickened, nematocyst-bearing area of the polypal wall. Occasionally in *Porites astræoides* tentacular disappearance, as contrasted with tentacular introversion, may be also observed.

Of previous observers, Fowler (1888, p. 11) has described and figured the introversion of the tentacles in *Seriatopora subulata*. Von Heider (1886, p. 158) has described in *Astroides calycularis* the opposite condition, in which the intertentacular portions of the disk have been drawn within the mesenterial chambers of the polyp, while the tentacles remain directed normally outward. The introverted disk in von Heider's figures presents in transverse and longitudinal sections much the same appearance as the introverted tentacles of *Porites* in figs. 30 and 40, that is, the ectoderm is internal and the endoderm external. In many instances of strongly retracted polyps the tentacles are found greatly depressed or introverted as integral parts of the disk. Discal infolding is noticed more fully on p. 434.

From all these examples it is manifest that the phenomenon of tentacular introversion in both expanded and retracted polyps, and of disappearance in the discal wall of fully expanded polyps, are very general among corals. They probably serve to explain the statements of some of the older observers that tentacles are wanting in certain species of corals.

G. von Koch (1890, p. 399) has found in the contracted polyps of the Alcyonarian, *Rhizoxenia rosea*, that, in addition to the infolding of the disk and upper part of the column, the tentacles undergo invagination, but only for about half their length; the proximal half still preserves the normal relationship of outer ectoderm and inner endoderm. This is undoubtedly similar to the process described above, only the introversion is not continued to the extreme limit, as in *Porites*. In the living expanded polyps of the coral *Astroides calycularis*, von Koch has also observed that the terminal part of a tentacle is often drawn inwardly toward the basal part, and again pushed out, the movements somewhat resembling the drawing in and pushing out of a telescope tube, and continuing for some time.

An explanation of tentacular introversion does not seem readily forthcoming, for beyond the usual ectodermal longitudinal and endodermal circular fibers no special musculature is discoverable whereby the movements may be produced; further, a decided individuality is exhibited by the various members comprised in the cycles. One may surmise as a cause a difference in the hydrostatic pressure between the internal cavity and the exterior, owing to variations in the circulation of the nutrient fluid within the colony. But this would not account for the fact that the polyp itself may remain fully expanded, and only certain of the tentacles be invaginated, while the others remain extruded.

The disappearance of the tentacular walls in the discal tissues seems more easy of explanation. Structurally the tentacles in the Madreporaria are rarely the important differentiated discal outgrowths which they have become in most Actiniaria, and when the polyps attain their full expansion it can readily be understood how the tentacular walls may become involved in the discal expansion, and lose the distinctness of their walls, the thick apex only remaining to indicate their former presence. The tentacles are originally outgrowths of the disk, and can again become part of it, the thickened apical knob remaining as the only evidence of a special differentiation.

Histology.—Histologically the walls of the tentacles present few characteristics which do not occur in the column wall or disk. Such peculiar features as they display have reference to their function as stinging organs. Transverse or longitudinal sections of most species exhibit marked inequalities in the thickness of the ectoderm, the broader regions representing special nematocyst areas. The thickenings correspond with the more opaque areas on the tentacular walls in the living condition, and are best seen in sections made from tentacles in the expanded condition, as in the retracted examples the wider nematocyst regions tend to overlap the intervening narrow areas (Pl. VI, fig. 50; Pl. X, fig. 75). The largest battery of stinging cells is at the apex, and here the outermost zone is constituted almost wholly of nematoblasts. By focussing with a high power around the free edge of a nematocyst area, triangular or thread-like cnidocils can usually be discerned, especially in the living tentacle, and cilia may be present over the whole tentacular surface (Pl. II, fig. 10).

The nematocysts in the tentacles are mainly of the long, narrow, thin-walled form, with the spiral thread closely coiled (Pl. XVII, fig. 124*a*). Other thin-walled forms—small and oval, or large and oval with a loose spiral thread—may occasionally occur, but are never so characteristic as the former. In the deeper parts of the ectodermal layer, brightly staining, apparently homogeneous bodies are generally seen, which represent nematocysts in various stages of development. At first they are irregularly arranged at almost every angle with the surface, but as they reach maturity they migrate to the periphery, and arrange themselves in a vertical direction, parallel with the other cellular constituents.

A weak longitudinal ectodermal musculature seems to be always present, the cut ends of the fibrils being displayed in transverse sections, and most pronounced toward the proximal extremity. In some species—e. g., *Cladocora*, *Madrepora*, and probably others—a distinct nerve layer also occurs, situated some distance from the mesoglœa (Pl. II, fig. 10 *nr. l.*). The ectodermal gland cells and supporting cells are practically the same as in the column wall, but the former are less numerous.

The tentacular mesoglœa is always a very thin layer, usually smooth on both surfaces, while the endoderm is comparatively broad with irregular internal limitations. The endoderm is generally richly supplied with zooxanthellæ, but the algæ are absent from *Phyllangia*, *Astrangia*, and certain of the tentacles of *Madrepora*. In all instances a weak circular musculature is developed, but the mesoglœa is rarely folded to afford it additional support, as in the larger tentacles of Actinians. The lumen is preserved, even in fully retracted tentacles.

The tentacles of several genera present so many peculiarities of form and arrangement as to call for special description.

TENTACLES OF MADREPORA AND PORITES.

The tentacles of the polyps of *Madrepora* and *Porites* are exceptional among the genera studied in that they are, with certain exceptions, only six or twelve in number, and in the adult usually exhibit constant variations in size. The tentacles of the apical polyps of *Madrepora* will be first described (fig. 1, *a*, *b*). In the most typical instances only six tentacles occur, all equal in size, and communicating with the entocœlic chambers. They are widest at their origin in the margin of the disk, where a considerable interval separates one from another, and terminate either acutely or in a rounded manner. The surface is smooth throughout, no urticating spots being visible.

Polyps with such a tentacular system are found at the apex of the long established branches of colonies of both the palmate and arborescent types of growth. On polyps at the ends of short, rapidly growing branches, rudiments of other tentacles also occur, alternating with the members of the first order. In regions of vigorous growth, as at the margin of palmate colonies, it is found that certain of the ordinary polyps, bearing the full complement of twelve tentacles, may become larger and assume an apical character, and among these the separation of the tentacles into an inner and an outer cycle can be recognized. Sometimes, only two or four of the six members of the outer cycle will be present, always much smaller than the entotentacles. All stages in the diminution in number and size of the outer exocœlic tentacles are, however, represented, according as the polyp has recently assumed or long maintained the apical position; at the same time, the six members of the inner cycle become larger and more equal.

From all the variations observed, it is clear that on any polyp taking on the axial condition the six exocœlic tentacles, present on all the radial polyps and smaller from the beginning, tend to completely disappear, and only the six entocœlic members ultimately remain, becoming at the same time larger and equal. Like the other regions of the axial polyp, the tentacles are perfectly colorless, owing to the absence of zooxanthellæ, and are not often seen fully expanded.

Among the fully developed radial polyps of *Madrepora* twelve tentacles occur; rarely, the number may be increased to sixteen, eighteen, or as many as twenty-four. The usual forms and arrangement are given on Pl. I, fig. 1 (*d.–n.*). The separation, as regards distance from the center of disk, into two alternating cycles of six each, is not clearly defined, but the members of one series are always larger than those of the other. The anterior or abaxial tentacle, adjacent to the nariform apex of the corallite, is longer and stouter than any of the others, and colorless, except toward its origin. It may be nearly twice as long as the others, and stands out very prominently; even in partly retracted polyps, when the tentacles are arranged vertically, it easily overtops the rest (*e.*). The opposite or axial tentacle—that is, the one adjacent to the stem—is the next in size, but differs very little, sometimes not at all, from the four large lateral tentacles. These four, two on each side of the median plane, are approximately equal. Later, in describing the relationships of the mesenteries of *Madrepora*, it will be seen that the large anterior abaxial tentacle is dorsal or sulcular in position, while the opposite axial tentacle is ventral or sulcar as regards the polyp as a whole (p. 444).

Of the smaller alternating series of six tentacles the abaxial laterals (one on each side of the large abaxial tentacle) are always the smallest, and are generally colorless throughout. The middle laterals come next in size, and the axial laterals may be a little smaller than these. The difference in size between the middle and axial laterals is, however, often scarcely perceptible; but the four are always larger than the two abaxial laterals, and are more deeply colored. In polyps near the apex of growing branches all the tentacles may be colorless.

As far as can be made out in the living state, the tentacles of the very minute, intercalary polyps are uniform in size, and in regions where the corallites possess a circular, free edge the tentacles tend to become more uniform in size. The large abaxial tentacle is always best developed in polyps where the corallite has the most marked nariform projection, as in *M. cervicornis*; undoubtedly, there is a relationship between the form of the mouth of the corallite and the amount of inequality among the tentacles.

In L. Agassiz's Report on the Florida Reefs (Pl. XVIII) an outline figure of an expanded terminal polyp of *Madrepora cervicornis* is given, in which six large equal tentacles alternate with six much smaller tentacles, likewise equal. Such a stage is occasionally met with on young branches, but is to be regarded as transitional to the stage in older branches with only six equal tentacles. On the same plate are also outline figures of expanded lateral polyps from near the tip of a branch; as there represented the abaxial aspect is uppermost.

Prof. A. E. Verrill (1869) was the first to draw attention to this variation in the external characters of the axial and radial polyps of *Madrepora*, and regarded it as the only instance of dimorphism among the Madreporaria. The apical polyps are seen, however, to be derived by modification of the radial, and, as will be shown later, the internal anatomy of the apical and radial polyps presents no differences corresponding with those of the tentacles, so that the dimorphism is not very deep seated.

The tentacles in all the West Indian species of *Porites* are, like those of *Madrepora*, usually twelve in number. Developing polyps exhibit a less number, and others occasionally occur in which the number may be fourteen, sixteen, or as many as twenty-four. On the colonies no distinction is to be made between apical and radial polyps. The tentacles of all the polyps are extremely small, smooth-walled, and digitiform, rarely exceeding 1 or 2 mm. in length. Viewed with a lens, in their fully expanded condition, or even when introverted, they appear to constitute but one cycle, and very often differences in size are recognizable of the same character as in *Madrepora* (Pl. IV, fig. 32). The two tentacles in the longer oral axis are somewhat larger than the others, and one of these, corresponding with the abaxial in *Madrepora*, is somewhat longer than the other; the tentacles situated one on each side of the largest are likewise the smallest of the twelve. Both *P. clavaria* and *P. furcata* exhibit this bilateral arrangement, but in such minute polyps the differences are not so decided as on the larger polyps of *Madrepora*, and are not obvious on all the polyps of a colony. In *P. astræoides* the twelve tentacles are usually equal in size.

It is shown later (p. 431), that this regular variation in the size of the tentacles of *Madrepora* and *Porites* is to be explained as the retention in the adult of a well-known larval stage passed through in the development of the tentacles of certain Actiniaria, and is also associated with a primitive condition of the internal mesenteries.

TENTACLES OF SIDERASTRÆA AND AGARICIA.

The tentacles on the polyps of the genus *Siderastræa* are so small as to be scarcely distinguishable with the naked eye, especially when retracted; but by careful examination with a lens their disposition and character can be made out. Observations have been made upon the organs in both *S. radians* and *S. siderea*. Instead of being closely arranged in a narrow peripheral zone, as in most corals and anemones, the individual tentacles are widely separated from one another, and occupy nearly the whole of the exposed polypal area (Pl. XXII, fig. 150). In the living condition each appears to arise either directly over or near the centripetal termination of the septum with which it corresponds. The cyclical arrangement is difficult to establish, and in many instances this would be impossible without the assistance from the septa which can be seen below through the soft tissues.

On full expansion the inner tentacles are found to consist of a short cylindrical stem, which bifurcates a little beyond midway, each half bearing a spheroidal enlargement at the apex; the outermost tentacles, however, are simple, consisting of a short stalk, terminated by a knob-like swelling (Pl. XXII, fig. 151). Thus in *Siderastræa* there is a true dimorphic condition of the tentacles, apparently the only instance of such among the Madreporaria, if we except the differences between the radial and axial polyps of *Madrepora*. In the course of the development of the young polyps (p. 533) it has been ascertained that the inner tentacles are at first simple, then afterwards another moiety arises over the same mesenterial chamber, and finally a common stem is produced, which bears the two halves at its extremity and raises them above the disk. Ontogenetically, therefore, the bifurcations represent distinct and separate formations, and only later constitute an entire tentacle.

Subsequent examination of sections confirms what would be expected from the external relationships, namely, that the bifurcated inner tentacles are all entocœlic in position, while the simple outermost tentacles communicate with the exocœles. In the nearly mature polyps of a colony, however, some of the entocœlic tentacles may be simple, but such are merely examples in process of development. The exocœlic members are never double.

On retraction of the polyps the disk and tentacles remain uncovered, the column wall in *Siderastræa* being incapable of overfolding. The tentacles are now represented by minute, simple and double tubercular enlargements, scattered over the greater part of the polypal wall. Microscopic sections reveal that the stems are no longer determinable as such, having become involved in the discal tissues, while the knobs remain as mere ectodermal thickenings (Pl. XXIII, figs. 154, 155). The apex of the exocœlic tentacles occurs as a simple swelling of the disk, directly overlying its corresponding septum, while the two knobs of the entocœlic tentacles are disposed one on each side of an entocœlic septal ridge, the two halves connected by a tissue similar to that of the disk, which manifestly represents the stem of the expanded tentacle. The ectoderm of the knobs includes a peripheral layer of long narrow nematocysts, and is thus easily distinguished from the rest of the disk.

Both *S. radians* and *S. siderea* are further characterized by the tentacles being apparently arranged in only approximate cycles, and by the occurrence of a comparatively wide interspace between one cycle and another. The imperfect cyclic disposition results from the presence of tentacles intermediate in position between the true cycles, and on the actual polyp it is often very puzzling, if not impossible, to say to which cycle some of the tentacles should be relegated. Polyps are found with from five to seven or eight tentacles, which, so far as their position is concerned, must be regarded as belonging to an inner cycle, and the remaining members seem to come in irrespective of any cyclic plan. In mature polyps of both species three more or less complete alternating cycles of tentacles are actually present, in addition to the outer single-knobbed cycle. The members of the latter being situated near the polygonal periphery of the polyp are rarely included within a circle.

When studied in conjunction with the underlying septa an approximate tentacular regularity can be established, as in fig. 150. The innermost cycle comprises six double-knobbed tentacles, separated by a wide interspace from the members of the second and third cycles, and these latter cycles are separated from the outermost cycle of single-knobbed tentacles. It is manifest from the figure that the tentacles correspond with the septa, and not all the twelve members necessary to complete the third cycle occur. *S. radians* appears to never complete its third cycle of mesenteries, tentacles, and septa, while in *S. siderea* it is occasionally reached or even exceeded. In fig. 150 only one member is wanting to complete the third cycle of entotentacles.

The apparent irregular disposition of the tentacles in this genus becomes explicable on a knowledge of the development of the mesenteries and their corresponding septa, or rather the two illustrate the same fact. In both species studied six pairs of perfect mesenteries form the first cycle, six alternating pairs make up a second cycle, and there may be twelve pairs forming a third cycle. As just mentioned, however, this last cycle is rarely completed. Further, an examination of the macerated skeleton shows that in very few instances is the full complement of septa, viz., 6, 6, 12, 24, present. Usually in *S. radians* only a few pairs of the third-cycle mesenteries occur, the number varying with the size of the polyp, while in the larger *S. siderea* nearly all the pairs are present, and even some members of a fourth cycle.

This incomplete cyclic development in the case of the mesenteries is repeated in the last cycle of entocœlic tentacles, and, the organs being widely apart, the imperfection of the cycle becomes more pronounced externally. With few exceptions the hexameral plan can be traced only as far as the first and second cycles. The third cycle may comprise any number of members from one to twelve, while the outermost cycle of simple tentacles contains the sum of the members of all the three inner cycles. Further, there is a tendency in most species of corals for the two inner cycles to constitute but one cycle of twelve, in the same way that as the polyps increase in size the mesenteries of the second cycle tend to unite with the stomodæum, and the first two orders of septa form only one cycle.

A considerable discal space intervening between the different tentacular cycles in *Siderastræa*, as compared with most other corals, it is clear that the two conditions alluded to above find their outward expression in individual tentacles occurring at varying distances from the center of the disk, and thus giving rise to the characteristic irregularity. In a fully developed, long-established polyp, the cycles are more regular than in a young individual. Moreover, were the cycles of tentacles in other coral species to be separated by such comparatively wide discal interspaces, instead of being arranged closely in a narrow zone, similar cyclic irregularities would be more generally noticed.

The arrangement of the tentacles in *Agaricia* very closely resembles that characteristic of the genus *Siderastræa*, but the organs are never bifurcated, and are not distinctly stalked. They remain exposed during the retracted condition of the polyp, and during ordinary retraction can usually be seen as mere pointed or triangular tubercles, but when expanded they become more digitiform, with an opaque white area at the apex. They are often brightly colored by comparison with the rest of the polypal wall. In several colonies of the form I identify as *Agaricia fragilis*, I was unable to determine the presence of any tentacles in the living condition, even with the aid of a lens. In sections through the disk they are, however, recognizable as slight, nematocyst-bearing thickenings of the ectoderm (Pl. XXIV, fig. 163). The organs are better developed in *Agaricia agaricites*.

As in *Siderastræa*, the individual tentacles are widely separated from one another, and are distributed over nearly the whole discal area, one above the apparent centripetal termination of each of the larger septa. No tentacles occur over the members of the smallest cycle of septa, which transverse sections demonstrate as exocœlic. In this absence of exocœlic tentacles the genus *Agaricia* is unique among the forms here studied, with the exception of the axial polyps of *Madrepora*.

The majority of the tentacles are arranged so as to form an inner cycle, but the number composing it is variable, and the cyclic character is only approximate. Outside there are a few scattered examples at different distances from the center, suggesting no cycle relationship. The number in the inner cycle varies from five to nine, while the total number in any polyp may be from thirteen to twenty-four.

In *Agaricia* mesenterial increase appears to be in constant progress, corresponding with the growth of the individual polyp, though in no regular cyclic manner. Similarly with the tentacles: the inner cycle includes all the older tentacles, and outside this are the later-formed members which appear irregularly. Probably it is best to regard the tentacles as acyclic, no exotentacles being developed. Counting the tentacles of many polyps gives odd numbers as often as even, while in the case of species with exocœlic tentacles even numbers predominate. The irregularity in the disposition of the tentacles in *Agaricia* should be compared with the irregular arrangement of the mesenteries represented on Pl. XXIV, fig. 161.

G. C. Bourne (1887), in his paper: "The anatomy of the Madreporarian coral Fungia," refers to the disposition of the tentacles in that genus. His figure of *Fungia* (Pl. XXIII) shows a wide interspace between the different cycles of tentacles, as is found to be the case in the much smaller polyps of *Siderastræa* and *Agaricia*. Evidently, the character may be taken as of some diagnostic importance within the Section Fungacea. Bourne casts suspicion upon the accuracy of Dana's description and figures of *Fungia* (Zoophytes, Wilkes Exploring Expedition, and Corals and the Coral Islands), which represent an irregular distribution of the tentacles at intervals over the whole of the large disk, as does also the figure of Quoy and Gaimard in Voyage de la corvette l'Astrolabe. The results from *Siderastræa* and *Agaricia*, detailed above, prove that an irregular appearance in the disposition of the tentacles is by no means uncommon in the Fungacea. The regular cyclic disposition, when really present, can often be established only after a long acquaintance with the forms, and under favorable conditions of expansion or retraction.

The figures of the fully expanded polyps of *Siderastræa*, accompanying Agassiz's Florida Reefs (1880, Pl. XV., figs. 6, 7), indicate an irregular tentacular arrangement in both cases, and such would probably be assumed by any observer on a casual acquaintance with the polyps. The appearances given the tentacles in Agassiz's figures were rarely met with in Jamaican specimens, but the dimorphism is clearly shown on some of the members, and is referred to by Pourtalès in "Deep Sea Corals" (1871).

ORDER OF APPEARANCE OF PROTOTENTACLES.

In corals whose development has been studied sufficiently far, the first tentacles are found to make their appearance within a few days after the fixation of the larva. The number of tentacles first to arise corresponds as a rule with the number of internal mesenterial chambers already established, the tentacles being outgrowths from them. Generally, in coral larvæ, the twelve primary mesenteries, with their corresponding chambers, are developed either at the time of fixation or shortly after, and the twelve primary tentacles appear either simultaneously, one from each mesenterial chamber, or one cycle may arise in advance of the other. In the latter case the inner cycle of entocœlic tentacles usually appears first, and the exocœlic members next, but in *Siderastræa radians* this order is reversed (p. 533).

The establishment of the tentacles serves to delimit for the first time the larva into two regions—disk and column; and with this the larva may be considered to have become the polyp. The part of the polypal wall bearing the tentacles and mouth is the disk, and the region outside or below is the column. The former becomes more or less flattened, and constitutes the free oral extremity of the polyp, as opposed to the fixed or basal aboral extremity, while the column is vertical and remains more or less cylindrical.

The actual appearance of the primary tentacles has been observed as follows: The larvæ of *Astroides calycularis*, examined by Lacaze-Duthiers (1873), presented twelve tentacular prominences at a very early stage after fixation. During the development of *Caryophyllia cyathus*, G. von Koch (1897) found that in most cases the two primary cycles of tentacles appeared simultaneously, though some of his observations seemed to indicate a successive origin. Von Koch's figure (p. 760) of the young polyp, at the stage when the prototentacles are all developed, represents the members of the inner entocœlic cycle as smaller than those of the outer exocœlic cycle, but in the text the author states that they are larger. Lacaze-Duthiers (1897), in his recent paper on the corals of the Gulf of Lyon, gives many figures illustrating the early development of *Balanophyllia regia*. From the beginning two alternating cycles of large and small tentacles are indicated, and no reference is made to any intermediate stage. The same author (1894) mentions six tentacles as occurring at an early stage in the development of *Flabellum anthophyllum*, and later figures the complete twelve.

Young polyps of *Manicina areolata*, which I was able to rear to the stage with twelve tentacles, were also characterized by the simultaneous development of these organs. When first definitely recognizable under the microscope, after a period of fixation of about fourteen days, two cycles were present, nearly equal in size (Pl. XIX, fig. 135). In two or three young polyps, from a batch of larvæ of *Favia fragum*, only six primary tentacles appeared simultaneously, about four days after the larvæ were set free, and in other larvæ reared later the members of the inner cycle appeared in advance of the outer (Pl. XIV, figs. 106, 107).

So far as I can discover, *Siderastræa radians* is unique among both corals and Actinians in that the first tentacles to arise are the six exocœlic members. This relationship was established in scores of instances, and no exceptions whatever were observed, so that it must be regarded as characteristic of the species. The six members were developed simultaneously a few days after fixation of the larvæ, and two or three weeks elapsed before the members of the entocœlic cycle began to appear. These were situated central to the first cycle, and in most cases the six appeared together, but a few exhibited a successive order, though of no regular character. For a long time the newer tentacles remained smaller than the older, the usual entacmæous order being thus reversed.

On the completion of the prototentacular stage, the relationships of the tentacles and mesenteries are as follows: The twelve primary mesenteries only have appeared, eight of which are complete and four incomplete, and the tentacles are outgrowths from the twelve mesenterial chambers, one from each. The six larger tentacles constituting the inner cycle are situated over the six entocœles, and the six smaller tentacles of the outer cycle over the six exocœles.

The rule that the tentacular sequence is associated with the stage reached in the mesenterial development was first demonstrated by Lacaze-Duthiers (1872) in the larvæ of *Actinia equina*. The primary mesenteries in this species were found to appear in bilaterial pairs, according to a regular sequence, and the tentacles conformed to this. Thus from the dorsal chamber, the larger of the two produced on the appearance of the first pair of mesenteries, appeared a large tentacle, and from the ventral or smaller chamber a smaller tentacle, both in the axial plane. As the later pairs of mesenteries arose and chambers were formed, corresponding tentacles appeared in a bilaterial manner until the twelve were established. The primary tentacles in *A. equina* retained the bilateral symmetry for some time, but ultimately this was succeeded by the adult condition, in which the tentacles in any cycle are equal in size.

All corals so far investigated, however, are provided with twelve fully established mesenteries (eight complete and four incomplete) and mesenterial chambers before the tentacles begin to make their appearance. Hence, there is rarely any successive development in their tentacular outgrowths, but the members of one or both cycles arise simultaneously—one from each chamber. Where in Actinian larvæ less than twelve mesenteries are present, the number of tentacles shows a corresponding diminution. Thus in larvæ of *Lebrunia coralligens* only eight of the primary mesenteries were developed at the time of fixation, and but eight tentacles appeared—in this case four large and four small. For nearly a week no increase of mesenteries took place, and the tentacles, though modifying their comparative size, remained of the same number. Some of the Actinian larvæ studied by Lacaze-Duthiers also showed only eight tentacles for some time, and Faurot (1895) has obtained similar results.

A few observations have been made upon the appearance of the tentacles in budding polyps. In the earliest stages determinable in buds of *Porites* and *Madrepora*, only six minute protuberances can be distinguished, two median and four lateral, differing somewhat in size. Older buds with eight or ten tentacles may also be found. Such instances merely suffice to indicate that the prototentacles of the bud do not arise simultaneously in the two genera mentioned, but in median and then in successive bilateral pairs. The buds, however, are so minute as not to permit of more detailed examination in the living expanded state, and scarcely anything can be ascertained from preserved colonies.

The bilateral condition of the tentacles in the adult *Madrepora* and *Porites*, already referred to, is full of suggestiveness from what is known of the tentacular development in the Actiniaria. Lacaze-Duthiers (1872) has shown that in *Actinia equina* an axial tentacle first appears, and that for a long time this remains larger than the others, which arise in successive bilateral pairs.[a] His

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[a] Dr. A. Appellöf (1900, p. 79) doubts the accuracy of Lacaze-Duthiers' account and figures of the development of the tentacles in *Actinia equina*, which have been accepted almost as classic. Among hundreds of larvæ of this species investigated by him, Appellöf has never met with the succession and proportional size of the tentacles indicated by

figure of the larva, at the stage where twelve tentacles are present, should be compared with the figures of the tentacles in the adult polyps of *Madrepora* and *Porites*, on Pls. I and IV. It is seen how very closely they agree in the relative sizes of the tentacles, and especially in the prominence of one of the axial tentacles (the dorsal of Lacaze-Duthiers, the abaxial of *Madrepora*); also, the small size of the tentacle on each side of this. Since the publication of Lacaze-Duthiers results somewhat similar phases in the appearance of the prototentacles have been obtained in other Actinians. In the Actinian, *Lebrunia corallígens*, I have shown (1899) that a bilateral stage with a large dorsal or sulcular tentacle is assumed even after a primary tetrameral radial phase. Occasionally anemones are come upon in which the primary large tentacle is retained in the adult, and in certain Sagartids occurring in Kingston Harbor the organ displays remarkable motile powers.

All the facts go to prove that the adult bilateral condition of the tentacles in *Madrepora* and *Porites* is to be regarded as the retention of a larval stage occasionally passed through by Actiniaria.

METATENTACLES.

No description is available as to the manner of appearance of the tentacles in any young coral polyp beyond the two cycles of prototentacles. The few observations I have been able to make indicate that the metatentacles appear practically simultaneously with the metacnemes, an exocœlic and an entocœlic member together, as in *Solenastræa* (fig. 83); or the entocœlic tentacle may arise in advance of the exocœlic, as in the young polyp of *Favia* (fig. 109); *Siderastræa radians* is again exceptional in that its exocœlic metatentacles arise before the corresponding entocœlic organs.

Very definite accounts of the order of appearance of the tentacles in Actiniæ are given by Professor Lacaze-Duthiers (1872), and also by Dr. L. Faurot (1895). By these writers it has been shown, in numerous instances, that the tentacles beyond the two first cycles arise in pairs, of which one member is entocœlic and the other exocœlic. The entocœlic tentacle grows more rapidly than the exocœlic, surpassing indeed the members of the outer (exocœlic) cycle of prototentacles. The exocœlic metatentacle attains the same size as the exocœlic prototentacles, and when the former are all developed the two series together are comprised in the third cycle, the second cycle now being formed of the entocœlic metatentacles, which rank next in size to the entocœlic prototentacles.

The stages passed through will be best understood from the accompanying figures (fig. 2), taken from Faurot's "Études." The process is that followed in *Tealia felina*.

ORAL DISK.

The oral disk is the more or less flattened distal termination of the polyp. It includes and is bounded peripherally by the tentacular zone, and bears the oral aperture in the middle. In most species the cycles of tentacles are closely arranged, and comprised within a narrow marginal region, while the more central area of the disk, known as the peristome, is naked, and may be depressed, flat, or elevated in a cone like manner. The tentacles on the disk of *Siderastræa* and *Agaricia* are comparatively widely apart, and the naked area is correspondingly diminished; the tentacular zone in *Orbicella acropora* also occupies a large proportion of the disk (fig. 1, p. 423). The discal walls are often delicate and partly transparent, and permit of the septa being seen through; like the column wall, the external surface may be smooth or verrucose. Usually numerous radiating grooves occur, corresponding with the internal mesenteries; the grooves of the complete mesenteries extend as far as the center of the disk, while those representing the incomplete mesenteries stretch only part way.

Lacaze-Duthiers; usually eight tentacles arise, practically simultaneously and equal. Knowing the great variability often exhibited by Anthozoan larvæ, according to the developmental stage at which they are extruded, it seems to me not unreasonable to suppose that even the same species may present such wide variations as those given by Lacaze-Duthiers and by Appellöf. The agreement of Lacaze-Duthiers' figures of *A. equina* with those representing the tentacles of *Madrepora* and *Porites* is certainly suggestive.

In simple polyps, and where asexual reproduction takes place by columnar gemmation, the disk is circular or slightly oval, and bears only one central mouth; a complete tentacular system belongs to each individual, and forms a closed circle. But where increase takes place by incomplete fissiparity the disk becomes large and irregular in outline, and as a rule bears more than one oral aperture, the whole surrounded by a complex tentacular system. In genera like *Manicina* and *Mæandrina* the disk is represented by irregular, meandering, flattened areas.

During the retracted state of the polyps the disk is depressed, its peripheral border resting upon the edges of the septa. On very strong retraction the interseptal discal areas may be drawn much below the level of the septal edges, and invade the polypal cavity as mesenterial funnels—"Septaltrichter" (see below). As a rule, the retracted disk is almost entirely hidden by the overfolding upper region of the column wall, but usually a small circular opening remains, simulating an oral aperture, and through it the middle of the disk can be seen below. On partial expansion also the disk may be sunk below the upper edge of the column, but on full expansion it usually becomes strongly convex, the middle area raised above the level of the column, and even of the tentacular zone. In *Favia fragum* the disk may project in this way as much as 5 mm., and the perioral region becomes extended in a dome-like manner, bearing the slit-like mouth at the apex. This is noticeable also in *Oculina diffusa* (Pl. XXII, fig. 149). In transverse sections through the disk thus produced only the complete mesenteries are usually included, as the incomplete members do not radiate far across (Pl. XI, fig. 83).

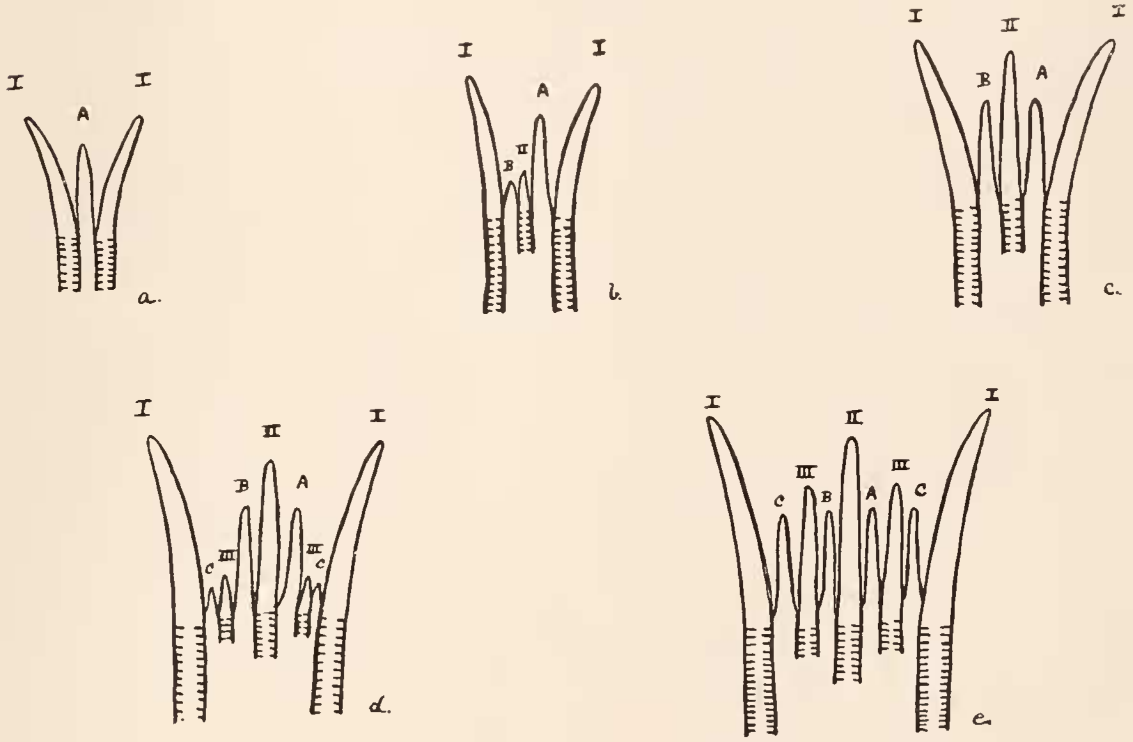

FIG. 2.

One of the six tentacular systems of an Actinian polyp, illustrating the order of development of the tentacles, from the stage with twelve to the stage with forty-eight tentacles, in their relation with the mesenterial chambers. *a*, Sextant with two entocœlic prototentacles (I, I) and one exocœlic prototentacle (A). *b*, Two rudimentary tentacles have appeared, one (II) from the entocœle and the other (B) from the exocœle of a new pair of metacnemes. *c*, The new entocœlic tentacle (II) has now become larger than either of the exocœlic tentacles, but is a little smaller than the entocœlic prototentacles (I), and constitutes the second cycle of tentacles, while the exocœlic tentacles (A, B) constitute the third cycle. *d*, Rudimentary tentacles (c, III; III, c) have appeared in association with the entocœles and exocœles of two new pairs of second-cycle metacnemes. *e*, The entocœlic tentacles (III, III), incipient in *d*, have now become larger than all the exocœlic tentacles, but are less than the member of the second cycle of tentacles, and constitute the third adult cycle of twelve tentacles. All the exocœlic tentacles (A, B, C, C), though appearing at different times, are now equal in size, and constitute the last or fourth cycle of the adult.

Histologically the disk differs but little from the tentacles or column wall. The peristome is generally very thin walled, and in nearly all cases is provided with weak radiating ectodermal and circular endodermal musculatures. Granular and clear gland cells are generally numerous, and nematocysts, somewhat similar to those in the tentacles, are sparingly distributed. In some cases a delicate ectodermal nerve layer can also be distinguished, but is never so pronounced as in the tentacles.

In fully retracted polyps of many species the discal wall is found partly introverted within the polypal cavity, somewhat in the same manner as already described for the tentacles (p. 423). Such a condition is often very confusing during the study of sections, and may seriously interfere with the determination of the relationship of the mesenteries to the stomodæum. In one important respect the invagination is distinguishable from the introversion of the tentacles; it is essentially mesenterial in position, while the tentacular inturning is intermesenterial. Pl. XVI, fig. 117, represents the appearance of the invaginations at different levels, as met with in a fully retracted polyp of *Dichocœnia*. The indentations occur about midway along the radial extent of the disk, and vary greatly in extent, but in general diminish from above inwards. The one to the left extends at this level over three mesenterial chambers, the entocœlic septum being evidently notched, and thus permitting of the continuity of two really distinct tracts. The middle invagination occupies only one exocœlic chamber, while the upper is still smaller, both in width and radial extent. The discal ectoderm is exceptionally broad, being cut obliquely, and the radial muscle fibers are clearly seen. The tentacles themselves are also involved in the discal invagination, but only as part of the disk, not as distinct organs.

The depression of the discal wall results in the interruption of the mesenteries radially, so that the latter are seen only toward their insertion in the polypal wall and in the stomodæal wall.

On Pl. XIII, fig. 95*a*, taken from a retracted polyp of *Favia fragum*, a discal introversion is seen near its termination, about midway along the transverse length of the mesentery; a few sections below, the continuity of the mesentery is established. Such an appearance might easily be mistaken for some tubular organ connected with a mesentery, but the phenomenon can be readily explained as a result of the strong contraction of the mesenterial musculature. It is easy to see how on full retraction of the polyp the discal wall will come to rest upon the septal edges; then any further mesenterial contraction can draw the interseptal portion of the disk only downward, so that in transverse sections the latter appears as if actually inclosed within the polypal cavity, along the same radius as the mesentery.

As already mentioned, von Heider (1886) has described an invagination of the discal wall in *Astroides calycularis*, but in this case the wall passes into the mesenterial chambers, without in any way involving the mesenteries. It is evidently independent of the action of these organs, and von Heider endeavors to explain the occurrence as dependent upon the interaction of the tentacles and expulsion of the water during retraction of the polyp.

Dr. O. Carlgren (1890), in his paper, "Giebt es Septaltrichter bei Anthozoen," discusses Goette's view that the mesenterial funnels (Septaltrichter) found in the young of various Actinian species are to be regarded as distinct organs. In the larvæ of *Bunodes gemmacea*, Carlgren obtained appearances exactly similar to those figured by Goette, and shows conclusively that they are merely contraction phenomena. Carlgren's figures compare most closely with figure 117, Pl. XVI, and leave no doubt that the appearances are all due to the same cause, namely, unequal contraction of different regions of the polyps during preservation. The occurrence of fixed septa in corals renders it much easier to understand how the inequality is possible in this group than in the case of the wholly soft-bodied anemones or their larvæ.

It may be conceived that the peculiar canal-like modifications, described by Fowler (1887), as occurring in certain mesenteries of *Madrepora durvillei*, have been produced by invaginations during strong retraction of the polyp. There are however, some features in this case different from conditions yet met with in corals, but on the other hand the modification seems altogether at variance with our present knowledge of their morphology.

MOUTH AND STOMODÆUM.

The actual form of the mouth of corals depends much upon the condition of expansion or retraction of the polyp. In the retracted or partly retracted state the aperture, as a rule, is narrow and slit-like while the outline assumed on expansion may be nearly circular. Under certain conditions the mouth is closed all the way, with the exception of a small opening at each extremity. In practically all cases a longer and a shorter axis are determinable, thus giving a bilateral character to polyps which otherwise would be outwardly radial in symmetry. In genera like *Manicina* and *Mæandrina*, with a meandering disk, bearing numerous small oral apertures, the longer axis of the latter is usually along the length of the disk, and the shorter axis is transverse. In branching colonies the longer oral axis is approximately in the axial-abaxial plane, while in the many polyps of compact flattened colonies it may be either radial or irregular in direction with regard to the middle of the colony.

The usual condition of living polyps is one in which the mouth is partly open, the white, smooth, depending walls of the stomodæum easily distinguishable through it. Rounded lips sometimes serve as a gradual transition from the disk to the stomodæum, but in deeply pigmented species the boundary between the disk and stomodæum is usually very sharply defined. When polyps are retracted, the mouth is generally in the same plane as the flattened disk, but on expansion it becomes more or less elevated along with the central part of the peristome (fig. 46).

The stomodæum is usually oval in transverse section, but may be circular. Its vertical extent, as a rule, is comparatively short, more so than is usually the case in Actinian polyps. In some species, the lower stomodæal edge can be easily discerned when the mouth is widely open, the organ suggesting a mere inturned flap of the disk. Sometimes the walls of the stomodæum are smooth, but in perhaps the majority of species they are thrown into deep vertical ridges and furrows, extending the whole length of the organ, and a little less marked in the fully expanded than in the retracted state. Generally the ridges are more noticeable on the living polyps than after preservation, and those of opposite sides alternate.

When the polypal tissues are partly transparent, the stomodæal ridges are seen to correspond in number and position with the attachment of the mesenteries to the inner or cœlomic surface of the stomodæum (Pl. XIX, fig. 131). To a limited extent, therefore, they serve to indicate the number of complete mesenteries. The ridges are found to be very variable in number in forms such as *Mæandrina*, *Manicina*, and *Isophyllia*, which happen to be species in which they are best developed. In *Mæandrina*, for example, only three or four ridges will be present on each side of the stomodæum where the oral aperture is small, while in others there may be seven or eight.

On transverse section the stomodæal ridges are seen to be formed by thickenings of the mesoglœa, and less so of the ectodem, but the endoderm takes no part (Pl. XXII, fig. 147). In species in which the ridges are best developed the ectoderm of the elevations exhibits a slight histological distinction from that of the furrows: large nematocysts and gland cells occur among the supporting cells of the former, while they are practically absent from the intervening areas, which on their part are more strongly ciliated. At the inner termination of the stomodæum the ridges appear as if continued down the free edge of the complete mesenteries as the mesenterial filaments, and the histology of the two agrees very closely.

With the exception of the ridges and furrows, occurring only in certain species, the stomodæal walls are structurally uniform all round; in other words, true gonidial grooves or siphonoglyphs are absent from Madreporarian polyps. As met with in the Actiniaria, at the opposite ends of the stomodæum, the gonidial grooves are readily distinguished in the living condition by the greater thickness and firmness of the walls, and by their smooth free surface; histoiogically the ciliation is stronger than elsewhere, and usually nematocysts and glandular cells are more sparingly distributed. The grooves in anemones are invariably associated with a pair of directive mesenteries.

A gonidial groove at each end of the stomodæum is, with certain exceptions, present in all Hexactiniæ; and a single groove occurs in the Zoantheæ and Ceriantheæ. In the Zoantheæ the organ is ventral or posterior, while, according to Carlgren (1893, p. 243), it is dorsal or anterior in the Ceriantheæ. A ventral groove, first termed by Professor Hickson (1883) the Siphonoglyphe, is likewise found in nearly all Alcyonaria. It is, therefore, a little remarkable to find that such a typically Anthozoan organ has never been established for the Madreporaria, and it is absent from each of the twenty-six species here studied[a]. Its non-development is probably indicative of the more primitive character of coral polyps generally compared with most Actiniaria.

The suggestion may be offered that the grooves, already described as occurring all the way round the stomodæum in some species of Madreporaria, are to be regarded as the morphological and physiological equivalents of the two axial grooves in the Hexactinian polyps. Instead of a groove occurring only between each pair of directives, one is found between all the complete mesenteries. The same histological differences are found in each case, though not so pronounced in corals. No experiments have been made to determine whether the grooves in the Madreporaria have any special function in directing the inhalent and exhalent currents, and with such small oral apertures experiments of this character would be difficult to conduct.

In living polyps of *Cladocora arbuscula*, *Solenastræa hyades*, and others, the lateral portions of the lips and stomodæal walls have at times been observed to come into close contact, leaving a small aperture at each extremity of the mouth, through which currents of water enter or leave the gastric cavity. A similar approximation has also been recorded by different observers as occurring among the Actiniæ, but is there associated with the presence of gonidial grooves. In the Zoanthidæ, provided with only one gonidial groove, only one terminal aperture remains when the lips are approximated.

The inner stomodæal extremity may become reflected upwardly and outwardly, so that in transverse sections the stomodæal walls are cut through twice; or, if they are much folded in addition, they may appear several times in succession in the same section. The appearance of the reflection in longitudinal section is shown on Pl. VII, fig. 56, and in transverse section on Pl. VI, fig. 51. The stomodæum terminates internally at practically the same level all the way round, or the two axial extremities, with the directives attached, may extend a little below the lateral walls, but nothing comparable with the "Languettes" of Actinians has been observed.

Upon complete retraction of the polyp, the distal parts of the polypal tissues—upper column wall and disk—mostly come to rest upon the skeletal projections—septa, pali, columella; in consequence of which the stomodæum becomes flattened and more or less irregularly folded. As a result it is often with difficulty that transverse sections of the stomodæum, exhibiting the relations of the mesenteries, can be obtained, especially as the organ is comparatively short.

On retraction the stomodæal walls as a whole are sometimes thrown into a few deep vertical folds, which assume a symmetrical figure. This is especially the case in *Porites* (figs. 28, 30); the folds may be four or six in number, and approach so as to touch one another in the middle, practically obliterating the lumen. The stomodæal foldings of a bud of *Cladocora* likewise assumed a regular arrangement (Pl. VIII, fig. 60); Fowler (1888) also describes and figures a similar appearance in a transverse section of the stomodæum of *Seriatopora sublata*. No doubt it is a consequence of the strong contraction of the circular endodermal muscle.

The histological details of the stomodæal wall are practically alike in all Madreporarian polyps, and agree closely with those of the Actiniaria. The ectoderm is always a broad, strongly ciliated layer, comprised largely of supporting cells, the nuclei of which are closely arranged, and give rise in sections to a characteristic, brightly-staining zone. The ciliation is uniform throughout, and is nearly always persistent in preserved material. As a rule nematocysts of two or three kinds occur, while both clear and granular gland cells are numerous. The latter are particularly abundant in *Cladocora* (fig. 52*b*). In some cases, e. g., *Phyllangia*, distinct ectodermal nervous and muscular elements can be made out near the mesoglœal surface, but are

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[a] Saville Kent refers to a siphonoglyp in a Barrier Reef *Fungia*, and Bourne adds one to his diagrammatic figure of a coral, on p. 62 of his article Anthozoa (1900).

never so pronounced as in the larger Actinian polyps. The histological differentiation where ridges and grooves are strongly developed has been alluded to above.

The ectoderm of the stomodæum terminates mesenterially in direct continuity with the mesenterial filaments of the complete mesenteries, and for some distance the histological details of the two are alike. The layer may be also partly reflected on the endodermal surface, and continued a short distance along the edge and both faces of the mesenteries (Pl. VI, fig. 51). This reflection of the stomodæal ectoderm plays an important part in discussions of the origin of the mesenterial filaments, and is again referred to on page 477.

The stomodæal mesoglœa is usually thin, and uniform in character all round. As a rule the endoderm presents no features which distinguish it from the same layer covering the whole of the upper part of the internal cavity.

COLORATION.

All descriptions of coral reefs allude to the great variety, richness, and beauty of color of the living coral. On any coral patch around Jamaica, the predominating colors are different shades of brown—light, dark, yellow, or green. This is largely due to the great abundance of colonies of *Madrepora*, *Millepora*, and *Mæandrina*, all of which exhibit one or other of these brown tints. Adding variety to these are the rich yellows, greens, and blues of the different species of *Porites*. Of the less massive corals—*Solenastræa*, *Cladocora*, *Oculina*, and *Favia*—yellowish-brown is likewise the prevailing color. Even where the general coloration of the colonies is nearly black or steel gray, as in some species of *Orbicella* and *Isophyllia*, a closer examination, especially when the polyps are fully expanded, indicates that yellowish-brown is the fundamental color.

The prevalence of the yellow-brown color is easily understood when an examination is made of the polypal tissues. For in all instances in which it occurs, the endoderm is found to be more or less crowded with the so-called "yellow-cells" or zooxanthellæ, which are unicellular symbiotic algæ, the chromophores of which are yellow or yellowish-green. That these are the main cause of the external coloration may be readily proved from colonies of *Madrepora*. In this genus the polyps toward the apex of growing branches are nearly colorless, the white skeleton showing through the perfectly transparent tissues, and on a microscopic examination of the endodermal layer zooxanthellæ are found to be absent, while they are present in abundance in the endoderm of the older, strongly pigmented regions. When a contracted living tentacle is viewed under the microscope, the margin is quite colorless as far as the thickness of ectoderm, while on focussing within, the endoderm is found to be almost black and opaque. The interior of fully expanded tentacles is lighter, and the individual yellow cells can be seen.

In the few instances in which zooxanthellæ are nearly or wholly absent from a species, as in *Astrangia solitaria* and *Phyllangia americana*, the polypal tissues appear peculiar delicate, and are wholly colorless and transparent, except for the occurrence of delicate superficial colors, such as rose and green. The transparency of the tissue appears to be very general in the members of this group of corals. In the "Introductory Notice" of the anatomy of *Astrangia danæ*, Fewkes (1889) also describes the color of the expanded polyps as "white, almost transparent, resembling an Edwardsia or small white Actinia; when contracted the color shows a green or bluish tinge." An examination which I have made of the tissues of this species reveals an absence of zooxanthellæ.

Again, the polyps on the under, unexposed surface of colonies living in shady places are nearly always devoid of color, although the individuals on the exposed area of the same colony are deeply pigmented. A remarkable instance of this occurs on the piles supporting the broad wharves at Port Royal. Numerous clumps of the corals *Oculina* and *Cladocora* grow attached to the piles; the outer exposed colonies are of the usual brown color, while those living on the inner pillars, which are cut off from the strong sunlight, are perfectly white, the corallum alone showing through the transparent tissues. It is manifest that a chlorophyll-bearing alga could not flourish under conditions where it is more or less deprived of light; but except for this absence of coloration the coral polyps appear normal. Colonies of *Agaricia*, which usually are densely colored, are found to be quite pale when living in the shady places often selected by these forms. The presence of zooxanthellæ does not seem to be at all essential to the life of coral polyps, seeing that colorless individuals in the shade flourish apparently as well as those in fully exposed places.

The degree of aggregation of the yellow cells likewise determines the intensity of the coloration. The tissues of fully expanded polyps are generally lighter in color and more transparent, and under these conditions zooxanthellæ are proportionately less numerous in a given area than during the retracted condition. When the polyps retract strongly, the algæ become closely aggregated within the thicker endoderm, and the tissues are darker and less transparent.

During the early stages of maceration of corals such as *Madrepora*, within a white porcelain basin, the zooxanthellæ will separate freely from the tissues, and accumulate on the bottom of the dish, giving to it a distinctly yellow appearance.

When coral polyps are preserved in alcohol a brownish yellow or golden yellow pigment is first extracted, but after a few hours, if transferred to colorless alcohol, the liquid is colored in the same manner as by the green coloring matter of plants.

The column wall and disk of the species of *Isophyllia*, *Mæandrina*, and less so of *Manicina*, *Colpophyllia*, and *Orbicella*, are often characterized by the presence of small, superficial, opaque, granular spots and patches. These are recognizable by means of a lens on the living polyps, and persist for some time after preservation. When the polyps are retracted the exposed tissues are practically opaque, and seem dense in comparison with the nearly transparent walls of such forms as *Madrepora*, *Oculina*, or *Cladocora*. The opacity is, however, limited to the regions of the column wall and disk which are fully exposed during retraction; the infolding margin of the wall, the tentacles, and the peripheral region of the disk, which are non-exposed regions, seem thinner and are more transparent. Any other marked superficial colors which may be present in these genera are likewise practically restricted to the exposed areas.

Examination of the outer tissues of these genera, by means of sections and macerations, reveals the presence of much finely granular, colored, non-transparent matter. The granular matter is mostly concentrated in the deeper regions of the ectodermal layer, but at certain points extends throughout the thickness, strongly distinguishing the areas from the remainder of the layer. Occasionally, as represented in the section of the column wall of *Isophyllia* (Pl. XVII, fig. 122), the accumulation occurs at fairly regular intervals. On the other hand, some regions, such as the upper margin of the column wall, the tentacles, and the periphery of the disk, are without the granular cells, these being the more transparent areas in the living polyp.

The small dense spots, referred to above as seen on the living tissues, evidently represent the points at which the granular matter is most concentrated, so as to extend throughout the thickness of the ectoderm, while the general opacity of the tissues is due to its more diffuse distribution within the deeper parts of the layer.

On maceration the contents of the cells appear as a finely granular substance, usually yellowish in color, and unacted upon, or only very slightly, by stains and acids. The cells thus differ from the more usual granular gland cells of the Zoantharia, which are always best developed toward the free surface of the layers, and take up stains, such as hæmatoxylin and carmine, with great avidity.

It may be conceived that the opacity has for its function the regulation of the amount of light passing to the endodermal tissues in corals living in more shallow waters. Certainly the forms in which the granular cells are best developed are among the least active of the coral polyps, and the coloration is most dense over the exposed areas. The endoderm shows no peculiarities which can be connected with the ectodermal opacity; zooxanthellæ occur as numerously as in other species.

Manicina areolata affords some interesting variations in the presence or absence of its dense superficial coloration, which seem to indicate some connection with the depth at which the corals occur. In colonies inhabiting very shallow waters, such as those of Kingston Harbor and Bluefields Bay, the superficial pigmentation—yellow, brown, or dense opaque white—is strongly pronounced, and in small or large irregular patches; but in young polyps and large colonies from the deeper water on the reefs this pigmentation is wholly wanting, and the tissues are of the more prevalent yellowish brown color, produced by the endodermal zooxanthellæ.

The superficial or ectodermal coloration of corals varies greatly within the same species, especially in different areas, and is of small importance for purposes of specific determination.

The polyps of *Dichocœnia stokesi* exhibit some exceptional conditions of coloration as regards the internal tissues. Within the ectoderm cells of the column wall are found highly refractive granules distributed throughout the layer with approximate uniformity. There is no evidence of the granules being aggregated within limited groups, nor of concentration toward the deeper regions of the layer. They are colorless in preserved material, but are green in the living polyp, and are no doubt the chief cause of the green color of the polyps, and the general opacity presented by the external tissues. On decalcification of preserved material the lower two-thirds of the embedded polypal tissues is also of a dark green color, contrasting strongly with the upper colorless walls. Microscopic examination reveals that, as usual, the lower skeletotrophic endoderm is greatly thickened, and densely crowded with granules of various sizes. Most of the particles, however, are a bright green, exactly recalling the chlorophyll granules in plants; in decalcified mounted sections the green color is still intense after two years. The granules in the gland cells of the lower region of the mesenterial filaments are also a strong green, and even the large nematocysts in the filaments have a green tinge.

Another form of pigment cell is found in the tissues of *Porites*. Some colonies of *Porites clavaria* are an intense bright yellow in their living condition, and a lemon color is often met with in living colonies of *P. astræoides*, while the polyps of *P. divaricata* as a rule exhibit only the pale brown due to the internal zooxanthellæ. Macerations and sections of polyps of the two first-mentioned species reveal that both the ectoderm and the endoderm are loaded with bright yellow, pigment-bearing cells, very variable in form and dimensions. So abundant are they in *P. clavaria* that in places it is almost impossible to make out any of the other histological elements; but in *P. astræoides* they are more sparsely distributed, and their relationships can be better determined. In general the chromophore cells are shorter than the supporting cells and gland cells of the ectoderm, and occur at all heights within the layer.

When the ectoderm is macerated the pigment cells separate somewhat readily from the other histological elements, and are very protean in shape, scarcely any two being of the same form. A few are represented on Pl. IV, fig. 37. The contents are very finely granular, and are scarcely affected by stains, but with borax carmine a very distinct nucleus becomes evident.

The chromophore cells occur most abundantly in the outer tissues, and in both ectoderm and endoderm, but are also met with sparingly throughout the polyp, including the epithelium of the mesenteries and communicating canals. Zooxanthellæ are found within the endodermal cells in their usual numbers. The polyps of the genus *Porites* vary in color more than any other form examined.

Another factor which probably influences the living appearance of many corals is the color given to the skeleton by the presence of perforating filamentous algæ, belonging to both the green and red groups. The coralla of all the species examined are found to be infested with boring algæ. After decalcification the filaments appear fresh and green near the surface, and contain protoplasm and chlorophyll granules, but are colorless and apparently dead in the more internal regions. So dense is the foreign growth that in some instances the superficial portion of the corallum is rendered bright green or pink by its presence, either wholly or in part. The skeletal color is best seen on freshly macerated specimens, as after a few months' exposure the coralla become more or less completely bleached. The upper superficial areas of the fresh corallites of *Orbicella* and extracalicular regions of *Colpophyllia* presented green patches of various sizes, while the color was usually more uniform in *Agaricia*, but almost any species of coral may exhibit large or small affected areas. Decalcification also proves that the perforating algæ may be present where a superficial examination of the corallum gives no indication.

By way of contrast with the more prevalent green color, the coralla of *Isophyllia dipsacea* after maceration of the soft tissues were a delicate pink, evidently from the presence of some red alga. This also gradually disappeared in the course of two or three months. *Siderastræa siderea* and *Porites astræoides* likewise often exhibit a bright pink color immediately below the surface of the corallum. In the latter it is still obvious on dried specimens twelve months after collection.[a]

Where the soft tissues of the polyps themselves are not densely colored, a green or reddish skeleton below must partly determine the general effect by reflection through the polypal wall. Lacaze-Duthiers (1897, p. 5) found the coralla of all the Mediterranean corals examined by him to be perfectly white when deprived of their soft tissues, hence concludes that the coloration is wholly polypal.

The surface of many polyps often presents a brillant emerald-green color, arranged in streaks or patches. It is found mostly on the disk as a peristomial ring, but occasionally on the oral aspect of the tentacles. Such has been observed in *Siderastræa radians*, *Orbicella annularis*, *Agaricia agaricites*, and *Colpophyllia*, as an addition to the more usual colors. The phenomenon is wholly superficial, not intracellular in origin, for histological examination fails to reveal any structure which can be assigned as its cause. The bright green and reddish colors of the otherwise colorless and transparent *Phyllangia americana* and *Astrangia solitaria* are also of this character, and pigment granules are here absent from the ectoderm, as well as zooxanthellæ from the endoderm.

The causes of coloration in living corals may be thus summarized:

(1) *Ectodermal.*—Pigment granules in ectodermal cells: aggregated in more or less isolated patches (*Isophyllia*, *Mæandrina*, etc.); generally distributed (*Porites*, *Dichocœnia*). Superficial.

(2) *Endodermal.*—Yellow cells or zooxanthellæ (nearly all corals); green granules (*Dichocœnia*); pigment cells (*Porites*).

(3) *Skeletal.*—Perforating green and red algæ.

MESENTERIES.

In all recent morphological studies, which have for their object the determination of the natural relationships of the Anthozoa, a greater significance is attached to the order of appearance and adult arrangement of the mesenteries than to any other polypal characteristic. These serve not only to limit the primary divisions of the group—Alcyonaria, Antipatharia, and Actiniaria, but in the Actiniaria the chief subdivisions—Hexactiniæ, Zoantheæ, Cerianthеæ, are likewise determined by the mesenterial features; and even for minor classificatory purposes the variations in the organs are often of great service. It will be found that a similar importance must be accorded the mesenteries in the Madreporaria, and dependent upon their arrangement is that of the tentacles and septa, as well as other less important relationships.

Among the adult polyps here studied, the simplest condition of the mesenteries is that occurring in the genera *Madrepora* and *Porites*. This is represented in transverse sections in the figures on Plates I and III, and, for the stomodæal regions, diagrammatically in the accompanying fig. 3. The latter will also serve as an illustration of the terminology to be employed, and also for certain cognate morphological considerations, which may be first considered.

In practically all the polyps of the two genera mentioned only twelve mesenteries occur, arranged in six pairs with regard to a median axis, which includes the longer diameter of the stomodæum. The four pairs reaching the stomodæum are known as complete mesenteries, while the two remaining pairs, not united with the stomodæum, are incomplete. The Roman numerals I–VI correspond with the established order of appearance of the pairs of mesenteries in coral larvæ to be described later.

The twelve mesenteries, characteristic of the adult *Madrepora* and *Porites*, occur also in the larval stage of genera of which the adults possess more than six pairs, and are strongly marked off by their mode of origin from the mesenteries subsequently developed; they serve, in fact, as the starting point for various types of mesenterial arrangement of the highest importance in Zoantharian studies. In 1900, I found it desirable to introduce some

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[a] The subject of coral boring Algæ has been more fully dealt with in a paper: "Boring Algæ as Agents in the Disintegration of Corals." Bull. Amer. Mus. Nat. Hist., Vol. XVI, 1902.

term which would distinguish these mesenteries, either singly or as a whole, from the later mesenteries. The twelve primary mesenteries constituting the first cycle were designated "Protocnemes," and those appearing later "Metacnemes."[a]

The appearance of a mesentery in transverse sections is rarely the same on both surfaces. The cut surfaces of the longitudinal or retractor muscle fibers form a bead-like margin to the mesoglœa, which is highly refractive and stains deeply (Pl. XVIII, fig. 129). Usually the longitudinal musculature on one face is stronger than the oblique musculature on the other, and as a rule the mesoglœa becomes folded or plaited to afford an increased area for the support of the former. The oblique muscle fibers are on the opposite face, and in transverse sections are usually cut obliquely, and the mesoglœa is rarely plaited for their support. For purposes of orientation, when studying the internal anatomy of the polyp, the recognition of the retractor muscle fibers on one face or the other of a mesentery is of great importance.

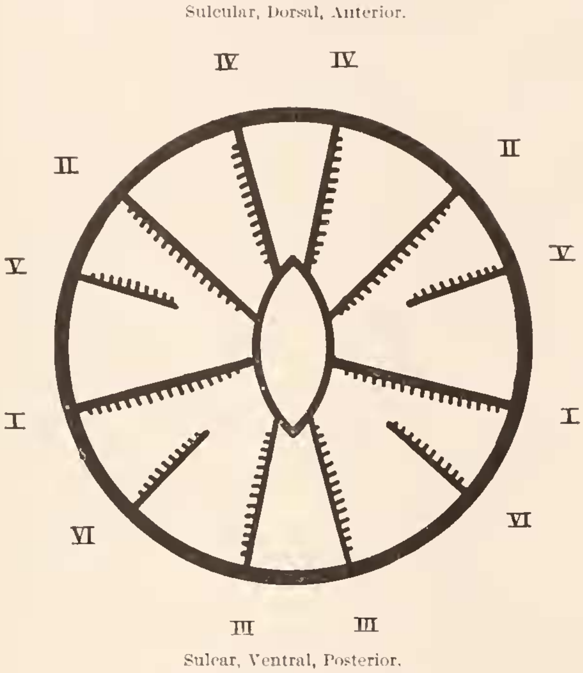

Fig. 3.

Plan of the mesenteries at the close of the protocnemic stage. The stage occurs in the growth of probably all larval and bud polyps, and is retained by most of the adult polyps of *Madrepora* and *Porites*. The Roman numerals (I-VI) indicate the order in which the mesenteries are found to appear in the larvæ of corals. The corresponding mesenteries on the two sides constitute bilateral pairs, and the adjacent mesenteries on each side in which the retractor muscles are turned toward each other (II, V; I, VI) constitute unilateral (anisocnemic) pairs; the members of the axial pair, III, III, are the sulcar or ventral directives, and the pair IV, IV the sulcular or dorsal directives. The vertical plane included within the two pairs of directives is the directive plane, and also the axial or median plane.

The mesoglœal plaitings for the support of the longitudinal mesenterial musculature are never greatly complicated in form in any of the coral species here studied. They may be quite simple, as on Pl. IV, fig. 38, or the folds may become secondarily plaited as in fig. 130. In the Actiniaria, on the other hand, the plaitings are often very finely subdivided in a dendriform manner, stretching along nearly the whole vertical face of the mesentery, or restricted about the middle to form a thick, broad, vertical band. The various figures given by Fowler, Bourne,

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[a] The substantive "κνήμη"—a radius or spoke of a wheel—was first employed in Anthozoan literature by Haddon and Shackelton (1891, p. 626) in the course of their studies of the Zoantheæ. In a foot-note with regard to it they write as follows: "We have tried hard to discover a short term for a mesentery, which would readily lend itself to combination with other words, but without success. The objection to the word 'cneme' is that it has reference to the appearance of a transverse section of an Actinian rather than to a mesentery as it actually exists. As the investigation of the Zoantheæ, at least, must principally be made by means of transverse sections, this objection has not much weight."

and other students of the anatomy of corals indicate that in other genera and species the muscle plaitings likewise remain comparatively simple.

The degree of complexity attained by the mesoglœal foldings undoubtedly varies much with the state of expansion or retraction of the polyp, the plaitings being often scarcely recognizable in the former condition. Their character also changes in different regions of the polyp, and even in different parts of the same section (Pl. IV, fig. 38). The mesentery of *Orbicella*, represented on Pl. IX, fig. 68, shows remarkable differences in this respect, the peculiarities extending even to the face bearing the oblique musculature. In the diagrammatic and semidiagrammatic figures throughout the paper the retractor muscle is conventionally represented by simple processes from the face of the mesoglœa.

From the figure on page 441 it is manifest that the paired character of the mesenteries may be regarded from two very different aspects. In the first place the corresponding mesenteries on the two sides of the median axis may be considered as pairs. These are known as "Bilateral pairs," and so far as concerns the first six pairs, this is the manner in which the mesenteries make their appearance in the larva. In bilateral mesenterial pairs the retractor muscle of each moiety is on the face turned toward the same aspect of the polyp. On the other hand, any two adjacent mesenteries in which the longitudinal muscles are on the faces turned toward each other—that is, toward opposite aspects of the polyp—may also be conceived as pairs, and, in contradistinction to the others, these may be known as "Unilateral pairs."

The two members of a unilateral pair may be either unequal (one complete and one incomplete, as in fig. 82) or equal (both either complete or incomplete, as in fig. 81). Considerations of much phylogenetic interest are connected with these conditions (p. 453). To distinguish a unilateral pair constituted of two equal mesenteries I propose the term "Isocnemic," and for a unilateral pair of two unequal mesenteries the term "Anisocnemic." In the majority of corals and anemones the metacnemes arise as isocnemic pairs, rarely, if ever, simultaneously by cycles, but bilaterally from one aspect of the polyp to the other (p. 459).

In most adult polyps the condition in which the longitudinal musculature of a pair is on the faces turned away from one another occurs only in the case of the two axial pairs, which by this means are distinguished as "Directives." Both from their origin and the disposition of the musculature, the directives are bilateral pairs, and are always isocnemic.

An attempt has lately been made to restrict the meaning of the nearly synonymous words "pair" and "couple," so as to imply whether the two moieties of a mesenterial pair are situated on the opposite side of the polyp, or whether they are close together on the same side of the polyp, their retractor muscles being vis-à-vis. Unfortunately, there is scarcely anything in the terms themselves to denote which should bear one special significance more than another, and already they are employed in a directly opposite manner by different Anthozoan writers. Thus Faurot (1895, p. 51), referring to the manner of appearance of the mesenteries beyond the primary twelve, writes: "Ces cloisons n'apparaissent pas par *couples*, comme dans la période précédente, c'est-à-dire, une d'un côté, une de l'autre côté de l'axe commissural de l'Actinie, mais par *paires* dans les interloges formées durant cette période. Il a été expliqué qu'une paire est constituée par deux cloisons voisines dont les faisceaux de feuillets unilatéraux se font vis-à-vis (les faisceaux unilatéraux des deux pairs commensurales faisant, seuls, exception) et que chaque pair forme une loge." Also van Beneden (1897, p. 21): "D'accord avec Faurot, j'estime qu'il y a lieu de réserver exclusivement le mot *paire* pour désigner deux closons voisines délimitant une loge; le mot *couple* pour dénommer l'ensemble de deux sarcoseptes symétriques, siègeant l'un à droite, l'autre à gauche du plan médian."

There can be not the slightest doubt as to the sense in which these authors employ the terms; a *couple* would be the arrangement corresponding with what is here termed a *bilateral pair*, and *pair* with what is here designated a *unilateral pair*. Yet Bourne, in the article "Anthozoa," in Lankester's "Treatise on Zoology" (1900, p. 39), in a foot-note adds: "It is convenient when speaking of the adult arrangement of the mesenteries to use the word 'couple,' when of their developmental sequence to use the word 'pair,'" thus signifying directly the opposite of Faurot and van Beneden.

Instead of adopting these familiar words, and giving to them a restricted meaning, and having to define whether the one or the other usage is to be attached to them, I prefer to speak of "unilateral pairs" and "bilateral pairs," according as the two moieties are situated on one side of the polyp, or are on opposite sides of the polyp. There can possibly be no ambiguity as to the character of the mesenterial pair indicated.

The portion of the gastro-cœlomic cavity included within a unilateral pair of mesenteries is, following the terminology proposed by Fowler (1885), known as an "Entocœle," while that between any two such pairs is an "Exocœle." Further, the polyp can be divided into sextants by six radii included within the primary entocœles, and the mesenteries or septa within each sextant are spoken of as constituting a "System."

A pair of directives occurs at each extremity of probably all sexually produced Madreporarian and Actiniarian polyps, but the regularity is often departed from in asexually developed polyps (p. 448). The vertical plane included within the two pairs of directives is known as the "Directive plane," and coincides with the axial or median plane of the polyp, as well as with the longer diameter of the stomodæum, and divides the polyp into symmetrical halves. Were the V and VI pairs of mesenteries to become complete, it is clear that a plane passing between the two pairs I and V would also divide the polyp symmetrically into equal halves, and include the shorter diameter of the stomodæum. Hence polyps at such a stage have two axes of perfect symmetry at right angles to each other. From the occurrence of directives, and of longer and shorter diameters of the stomodæum, perfect radial symmetry is not found in any of the present species, and where noticed elsewhere is probably a result of asexual methods of reproduction—not a fundamental characteristic.

Among animals like coral polyps and anemones, exhibiting a certain degree of radial symmetry, the terms dorsal and ventral and anterior and posterior, though adopted, have not the same significance as in the higher animals, where one aspect of the body is altogether different from the other. Moreover, the relationships, even as understood, are not readily established in adult polyps. To determine them it is necessary to select some morphological condition to which the disposition of the organs can be referred. The presence of directives enables a median plane to be established, to which the organs on each side of the polyp are symmetrically related, right and left, and such a mesenterial stage as that represented on page 441 also enables what may be termed upper and lower borders to be established. The aspect of the polyp toward which the faces bearing the longitudinal musculature of the two complete bilateral pairs of mesenteries I, II are turned has been designated by Haddon (1889, p. 300) the "Sulcar," and the opposite the "Sulcular." The terminology is based upon the fact that amongst Anthozoa where only one gonidial groove (sulcus) is present (Alcyonaria, Zoantheæ), the organ is on the aspect of the polyp toward which the faces of the two pairs of mesenteries, referred to as bearing the vertical musculature, are directed. As gonidial grooves, however, seem never to occur within the Madreporaria, this character is of no assistance for purposes of orientation, and the sulcar and sulcular relationships, as a rule, can only be determined from the order of development of the first cycle of mesenteries. Where, in Zoantharian polyps, all the six pairs of protocnemes are already complete, and either no gonidial grooves are present or both are equally developed, there is in ordinary cases no means of determining the sulcar and sulcular relationships. By most writers on the Anthozoa the sulcar border is regarded as ventral and the sulcular as dorsal.

Is it possible to determine an antero-posterior relationship in the polyps from the known facts of their development, such as shall be at all comparable with that in the higher animals? E. van Beneden (1891), from his study of the development of the Cerianthid *Arachnactis*, and E. B. Wilson (1884), from his investigations on the mesenterial filaments of the Alcyonaria, follow the suggestions of Sedgwick and Caldwell, and compare the gastro-cœlomic chambers of the Anthozoa with the cœlomic diverticula of the higher animals. On this theory the side of the Cerianthid polyp on which the sulcus and directive mesenteries are situated is regarded as anterior, while the side at which new mesenteries or segments are added is considered to be posterior. From the arrangement of the mesenterial musculature, Carlgren (1893) has shown that the sulcus of *Cerianthus* is situated at the opposite extremity of the polyp from its position in the Alcyonaria and Zoanthidæ. If the sulcar aspect in all Anthozoa except *Cerianthus* be conceived as ventral, then in the latter it will be dorsal as well as anterior, and the ventral or sulcar aspect in other Anthozoa is posterior. It is shown later that the general succession of growth of the mesenteries in Madreporaria is also from the dorsal to the ventral aspect of the polyp, that is, they arise in an antero-posterior order. The septa have also been found to follow a like succession.

The relationships may be thus compared:

Hexactiniæ, Zoantheæ, Madreporaria	Sulcar =ventral=posterior. Sulcular=dorsal =anterior.
Ceriantheæ	Sulcar =dorsal =anterior. Sulcular=ventral=posterior.

Where coral polyps present a definite relationship to the axis of a branch, as in most species of *Madrepora*, *Oculina*, and *Cladocora*, axial and abaxial positions are further determinable; and in the rounded colonies of *Orbicella*, *Solenastræa*, etc., inner and outer relationships, which correspond with axial and abaxial, are also distinguishable. Some importance underlies these determinations, for it will be found that the axial-abaxial and sulcar-sulcular relations are not always the same in corals.

The relationships of the strongly bilateral, radial polyps of *Madrepora* to the axis of the colony may be first determined. The transverse section on Pl. I, fig. 4, represents the polyp as situated in relation to the axis of the branch, but the lower side in the figure is inner or next the axis, and the upper is outer or turned away from the axis. Owing to the nariform growth of the corallite the skeletal tissue is more thickly developed on the upper than on the lower aspect. From the proportional development of the mesenteries, and the disposition of the longitudinal musculature, it is clear that the axial or inner aspect is the sulcar, and the abaxial or outer aspect the sulcular; or, in the terminology usually adopted, the former is ventral and the latter dorsal. The large anterior tentacle of *Madrepora* thus communicates with the sulcular, and the posterior tentacle with the sulcar entocœle.

Wherever in other corals it has been possible to determine the sulcar-sulcular relationships, as well as the axial-abaxial, to the colony as a whole, it is found that the relationships prevailing in *Madrepora* are reversed. Thus on Pl. VIII, fig. 61, representing a bud of *Cladocora* with the protocnemes in the *Edwardsia*-stage, the sulcar aspect of the polyp is abaxial or outward, and the sulcular is axial or inwards, in relation to the colony; similarly in fig. 62, representing another bud of the same species. In fig. 87, Pl. XII, taken from a young bud of *Solenastræa*, the sulcar side of the polyp is again outward (abaxial) and the sulcular is inward (axial).

Dr. G. H. Fowler (1887), in his studies of *Madrepora durvillei* and *M. aspera*, was the first to determine the axial-abaxial relationships of the mesenteries in the genus, and the year following (1888, p. 12) he showed that it was directly the opposite of that occurring in *Seriatopora subulata*, the polyps of which also permit of axial-abaxial determinations. The difference between *Madrepora* and other corals can best be appreciated by comparing the diagrams on page 445.

Dr. Carlgren (1896) has shown that in colonial Zoanthidæ the macro-directive mesenteries and the single gonidial groove are on the outermost side of the colony, or farthest from the mother polyp, while the micro-directive mesenteries and asulcular extremity of the stomodæum are toward the inner side of the colony, or nearest the parent polyp; the anterior (dorsal, asulcar) part is directed toward the axis of the colony, while the posterior (ventral or sulcar) is turned away from it (fig. *c*). The relationship of the individual polyp to the Zoanthid colony is therefore in strict conformity with that in Madreporaria, the genus *Madrepora* excepted.

The researches of Moseley, Hickson, and others on the Alcyonaria have also demonstrated that in this group the relationship of the polyp to the axis is the same as that in most Madreporaria. The so-called ventral aspect (sulcar) of the Alcyonaria is abaxial, the dorsal aspect (asulcar) is axial (fig. *d*).

The stage of mesenterial development with only four pairs of complete mesenteries usually serves the larvæ of Actiniaria and Madreporaria as a resting stage for a long period. Among the Actiniaria the only forms known in which the adult was thought to remain at this simple stage are the Edwardsiæ. The resemblance between the mesenteries characteristic of this group, and those appearing in the course of the development of the Actinian larvæ, was recognized by Haddon (1889), and the stage was termed by McMurrich (1889) the "*Edwardsia*-stage." The eight complete mesenteries, comprising two bilateral pairs (I, II) and two pairs of directives (III, IV), are often spoken of collectively as the Edwardsian mesenteries.

Until recently the adult *Edwardsia* was supposed to have no other than these eight complete mesenteries, and in this respect was considered to be one of the simplest of the Actiniaria. As such it has been regarded by Boveri (1889) and McMurrich (1891) as the starting point for the diverse modifications occurring within the different Actinian groups. Lately Faurot (1895), by making transverse sections through the uppermost region of the capitulum of *Edwardsia beautempsi*, has shown that in this species sixteen and even twenty mesenteries are present, corresponding with the same number of tentacles. The eight additional mesenteries were found to be feebly developed, but arranged on the normal Hexactinian plan, and to extend vertically

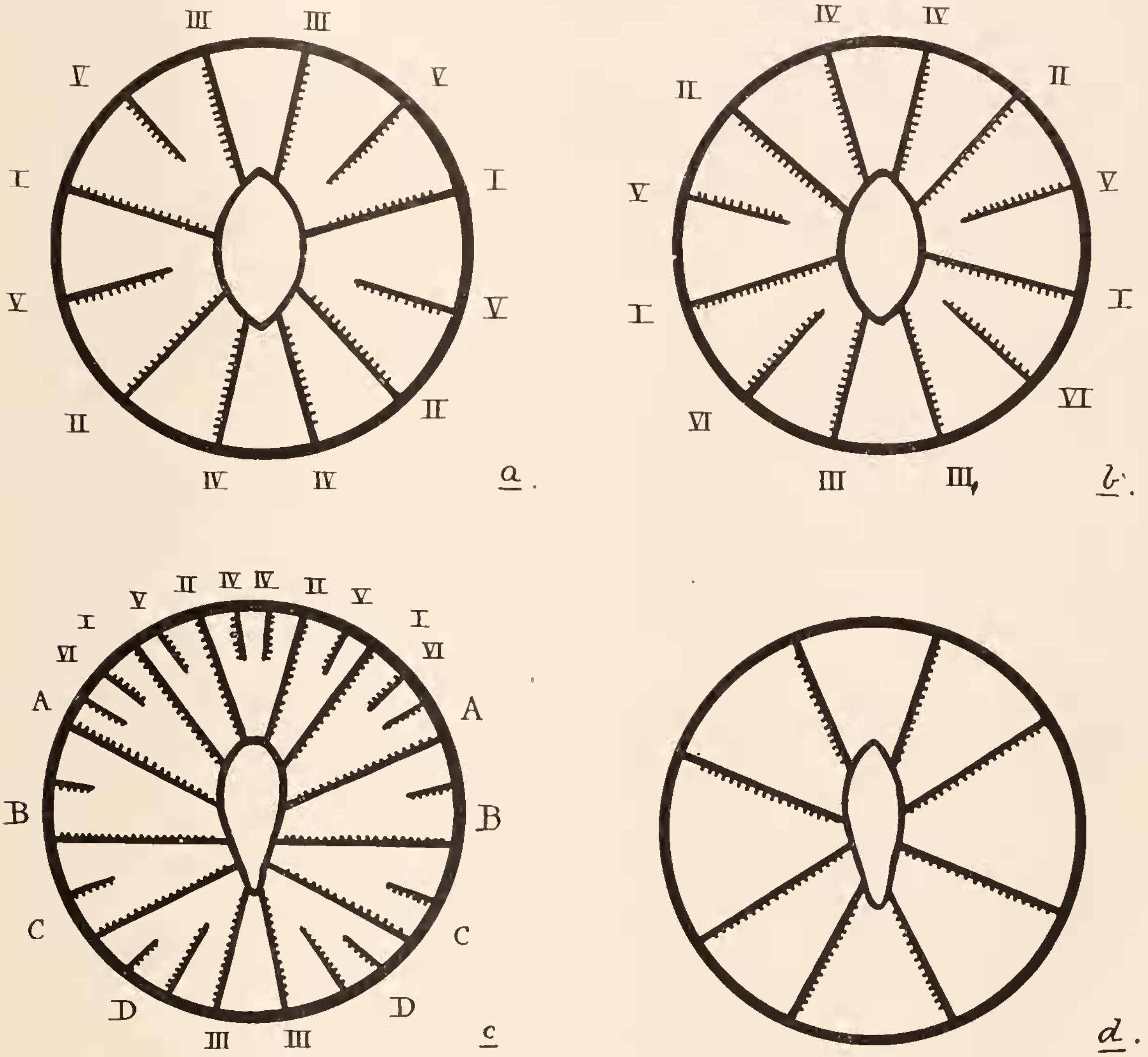

FIG. 4.

Diagrammatic figures showing the relationship of the polyps to the axis in various colonial Anthozoa. The upper side of the figure is supposed to be toward the axis (axial) and the lower is away from the axis (abaxial). *a*, *Madrepora*. The sulcar or ventral aspect of the polpy is axial and the sulcular or dorsal is abaxial. (The upper of the two bilateral pairs marked V, V should have been VI, VI.) *b*, Most other Madreporarian species. The sulcular aspect is axial and the sulcar abaxial. *c*, Zoanthids. The gonidial groove or siphonoglyph is abaxial, and all the metacnemes (A–D) are added at this aspect. *d*, Alcyonaria. The siphonoglyph is abaxial.

only for about half a centimeter. Four of these, along with the eight complete mesenteries, constitute the six pairs of protocnemes, while the remaining four represent a pair of metacnemes within each dorsal or sulcular exocœle. Notwithstanding this discovery, it is deemed convenient to retain the term "*Edwardsia*-stage" for the condition in which only the first four protocnemic pairs are complete, whether other mesenteries are present or not.

The fewness of the mesenteries in *Porites* and *Madrepora* readily permits of their vertical order of appearance and disappearance being followed in serial transverse sections, but the same can be carried out also in more complex, multicyclic forms. In species with a large number of mesenteries the pairs are developed from above downward, as in *Porites* and *Madrepora*, so that the greatest number of cycles occurs in the more distal region of the polyps, and the members of the last-formed cycles often traverse but a slight vertical extent, compared with that of the oldest cycles. During the development of the mesenteries it is found (p. 454) that while the first two or three pairs arise at or near the uppermost extremity of the polyp, that is, around the oral aperture, the later pairs first appear some distance down the column wall, thence grow in both directions, upward and downward.

The mesenteries in adult corals as a rule terminate before the lower aboral extremity of the polyp is reached, hence this region is altogether unoccupied by any of the polypal tissues, except those lining the skeleton (Pl. IX, fig. 67). The organs rarely occur below the upper half or two-thirds of the vertical height of retracted polyps. Below, however, the septal invaginations extend farther centrally than above, and the skeletotrophic endoderm becomes enormously thickened, so that aborally the cœlomic cavity is greatly diminished in extent.

The restriction of the mesenteries in corals to the upper regions of the polyp should be compared with the extent of their course in Actinians. Here the principal mesenteries usually traverse the whole length of the column wall, and then extend across the basal disk toward the center, where they often meet. On the other hand, it must be remembered that the aboral extremity of the Madreporarian polyp does not altogether coincide with that of the Actiniarian polyp. In the former, part of the basal disk is greatly invaginated, and its peripheral border, where it passes into the column wall, is raised much above the actual extremity of the polyp.

Perithecally the mesenteries may extend the full length of the column wall or edge-zone (*Orbicella*, *Solenastræa*, etc.), or may terminate in advance of it (*Oculina*). In the latter case the attachment to the skeletotrophic tissue may be the first to cease, that on the column wall remaining, or the columnar attachment may be the first to disappear. In *Cladocora* the mesenteries rarely extend in a complete manner the whole length of the peripheral chambers, the skeletotrophic attachment ceasing first (Pl. VII, fig. 54).

The mesenteries in *Siderastræa* are characterized by a peculiar resorption of the peripheral extremities, so that in the more central part of the polyp the organs extend much farther vertically than in the peripheral region (Pl. XXIII, fig. 153).

The polyps available are generally so small as not to permit of the mesenteries being readily dissected out and viewed as a whole; but in serial transverse sections no interruptions suggestive of *mesenterial stomata* have been encountered. Hence there is good reason to suppose that mesenterial stomata are absent from Madreporarian polyps. The continual growth upward of the polyp, and the resorption of the mesenteries below, characteristic of most species, would in all probability preclude the formation of such characteristic Actinian features.

MESENTERIES IN GENERA REPRODUCING BY BUDDING.

The adults of all other polyps here described are provided with a greater number of pairs of mesenteries than the primary six of *Porites* and *Madrepora*. In the genera *Orbicella* (p. 423), *Solenastræa* (Pl. XI), *Oculina*, *Siderastræa* (Pl. XXIII), *Cladocora* (Pl. VI), *Astrangia* (Pl. VI), and *Phyllangia* (p. 464), which reproduce asexually by budding, the mesenteries are arranged in alternating hexameral cycles, and vary in size according to the cycle to which they belong. The designation "cycle" is employed to include all the mesenteries having the same radial extent, while the term "order" has reference to mesenteries which appeared at or about the same time; the first has reference to their insertion on or distance from the stomodæum, and the second carries with it a developmental significance. Thus the members of the first order always appear before those of the second, the second before the third, and so on. Should the first cycle consist of twelve mesenterial pairs, as is sometimes the case, it represents the first and second orders. The members of the first order are known as primaries, the members of the second order as secondaries, the members of the third order as tertiaries, and so on.

In the genera above mentioned the first order or cycle of six pairs (protocnemes) includes the same mesenteries as those present in *Porites* and *Madrepora;* but usually all the pairs are complete and equal, and in each case they include two pairs of directives—sulcar and sulcular, which are bilateral, and situated at opposite extremities of the polyp; the other four protocnemic pairs, notwithstanding their origin as bilateral pairs, are now regarded as four unilateral pairs, two on each side, the retractor muscles of each pair being on the faces turned toward one another.

The second order of mesenteries in adult polyps also consists of six equal unilateral pairs, alternating with the pairs of the first order, and situated within their exocœlic chambers. In some cases the pairs of the second order may become complete throughout the whole or part of the extent of the stomodæum, as in the large polyps of *Orbicella cavernosa;* or some of the pairs of the cycle may be complete and the others remain incomplete, as in the polyp of *Phyllangia*, represented on p. 464.

When fully developed, the third order of mesenteries comprises twelve unilateral pairs, within the exocœles formed by the pairs of the first and second orders. The fourth order of mesenteries would contain twenty-four pairs, the fifth forty-eight, and so on, the mesenteries of the newer cycles always occurring in unilateral pairs within the exocœlic chambers of the previous pairs. The fourth-order mesenteries, however, never appear in any of the species here studied, except in *Phyllangia*, where occasionally a few members may occur (p. 465). Very often the mesenteries present in any mature polyp may be such as to leave the last cycle without the full number of pairs necessary to complete the hexameral sequence.

Although in the adult polyp the metacnemic pairs belonging to any cycle are approximately equal in size, it by no means follows that they were simultaneously developed, any more than in the case of the pairs of protocnemes; indeed, all the evidence from young polyps goes to show that the mesenteries arise successively. The order of appearance of the metacnemes is fully referred to on p. 455, *et. seq.*

The mature polyps of the species belonging to the genera enumerated contain, within narrow limits, a definite number of mesenterial pairs, which is characteristic of the species. As above mentioned, this number may or may not complete the hexameral multiple, so that the last cycle commenced may not be continued all the way round.

Increase in number does not continue indefinitely. *Orbicella acropora* has usually twelve pairs of mesenteries, six complete pairs of protocnemes, and six alternating incomplete metacnemes; *O. radiata* contains twenty-four pairs, the twelve pairs of the first and second orders complete and otherwise equally developed, and the twelve pairs of the third order incomplete (fig. 1, p. 423); the conditions are the same in *O. cavernosa.* The mesenteries of *Solenastræa* and *Oculina* are, like those of *O. acropora*, usually twenty-four in number, six pairs complete and six alternating pairs incomplete (Pl. XI, fig. 81).

Astrangia solitaria exhibits six pairs of complete mesenteries, and within each primary exocœle of adult polyps a pair of incomplete mesenteries always occurs, and in some instances two or three pairs (p. 463). In this latter case one of the pairs is slightly larger than the other and belongs to the second cycle of six pairs, while the smaller pair represents all that is yet developed of the third cycle; but in no instance has the full complement of twelve pairs constituting the third cycle occurred. In the closely allied species, *Phyllangia americana*, the number of mesenteries is always greater; but here also the incompletion of the final cycle of twelve pairs is very general. In one polyp sectionized transversely (p. 464), ten pairs of mesenteries reach the stomodæum. These consist of the six protocnemic pairs and four of the first-cycle metacnemes, the remaining two of this cycle not having yet reached the stomodæum. In the uppermost stomodæal region, however, one of the pairs becomes complete. An alternating cycle of twelve incomplete pairs occurs, but one or more pairs may be rudimentary or absent.

The adult polyps of *Cladocora arbuscula* always contain six pairs of complete mesenteries, constituting a first cycle, and six alternating pairs which remain incomplete and form a second cycle. Representatives of a third cycle are usually developed, but instead of consisting of twelve pairs, one in each exocœle between the previous twelve pairs, only four or six pairs are usually present, all on the same aspect of the older pairs (Pl. VI, fig. 49). Earlier stages in the development reveal that this is probably the sulcar aspect of each system (p. 458).

In *Siderastræa radians* six pairs of complete mesenteries are present, along with six alternating incomplete pairs, and a few pairs belonging to the third cycle may also occur; usually the third-cycle pairs are radially shorter than those of the second cycle, but at other times they nearly equal them in size. In the larger species, *S. siderea*, though more members of the third cycle are present, the whole twelve pairs necessary to complete the cycle are rarely present (Pl. XXIII, fig. 153).

The polyps of the seven genera described, all produced asexually by the process of gemmation, are thus characterized by the very regular disposition of the mesenteries in alternating hexamerous cycles. The first and second cycles are fully developed in all the adult polyps, while the third cycle may be only partly formed, but so far as it goes the members alternate regularly with the other pairs, according to the order of appearance established on p. 455 *et. seq.* In all the polyps two pairs of directives occur in the first cycle. So far as the mesenterial arrangement is concerned, there seems no difference between a polyp originating as a bud and one derived from a sexually produced larva; both follow the normal hexactinian plan.

Only the members of the first and second orders ever become inserted on the stomodæum in the species studied. The later orders never become complete, but retain a definite size characteristic of the species.

MESENTERIES IN GENERA REPRODUCING BY FISSION.

The asexual reproduction of the following genera takes place mainly, if not entirely, by stomodæal fission: *Agaricia*, *Isophyllia*, *Dichocœnia*, *Favia*, *Manicina*, *Mæandrina*, and *Colpophyllia*. In the first four the polyps so produced may become more or less distinct from one another, each with its own system of tentacles and a column wall; in the remaining genera the separation is incomplete, and meandering discal, tentacular, and columnar systems are produced in place of distinct polyps, and only exceptionally are transverse walls developed, which separate one series of oral apertures from another. Sections have been made through polyps of each of the above genera, and reveal a mesenterial arrangement very different from that already described for genera where asexual reproduction by gemmation is the rule.

Transverse sections through two polyps of *Agaricia fragilis* are represented on Pls. XXIV and XXV, while the arrangements of the mesenteries of two different polyps of *Isophyllia* are diagrammatically shown on next page. Fundamental differences are at once apparent, compared with the mesenterial plans already described. No directive mesenteries occur in these nor in any of the other examples studied Very rarely the number of complete pairs may be six, but is usually irregular, while the incomplete mesenteries vary greatly in number, size, and relation to the complete pairs. The hexameral plan is altogether departed from, and each stomodæum may have from ten to twenty-five complete mesenteries associated with it. A regular alternation of second and third cycle mesenteries is found in only one or two places, as at the upper right-hand region of fig. *b*; here and there a single unpaired mesentery may occur within an exocœle. Of the many polyps of each species examined no two display exactly the same number and relationship of the mesenteries.

A like absence of hexameral, or any other, regularity occurs in the polyps of *Dichocœnia* and *Favia* (Pls. XIII and XVI). Transverse sections reveal a variable number of pairs of perfect mesenteries from four upward, according to the size of the polyp, while the alternating incomplete pairs are rarely the same in number and size in any two exocœles, and no directives occur.

In sections of mature colonies of *Manicina areolata* only two series of mesenteries can be generally distinguished, complete and incomplete, the latter rarely affording evidence of alternating second and third cycles. The number of mesenteries associated with the stomodæal systems is very variable, and in any colony, however large, there are probably only two pairs of directives, situated at what may be regarded as the morphological extremities (p. 507).

Compared with the cyclical complexity in *Favia*, *Manicina*, etc., the mesenteries of *Mæandrina* and *Colpophyllia* exhibit a remarkable simplicity of arrangement (Pl. XXI, fig. 141). Practically all the pairs are complete, and may be regarded as belonging to a single order; here and there alternating incomplete pairs are met with, but it is impossible to establish a regular succession of complete and incomplete pairs. Never more than one or two alternations occur together, while frequently six or seven consecutive complete pairs may be passed in review, all apparently of equal value, and all bearing filaments. The incomplete pairs in all probability represent new pairs in process of development, which will ultimately become complete like the rest. From eight to sixteen mesenteries may be inserted on each stomodæum, according to the size of the oral aperture; apparently there is no regularity in the number of mesenteries which upon fission may be apportioned to each daughter stomodæum. In the living colony a small oral aperture with only seven or eight complete stomodæal ridges, representing so many mesenteries, may appear as if just cut off from another large aperture with a dozen or more stomodæal ridges.

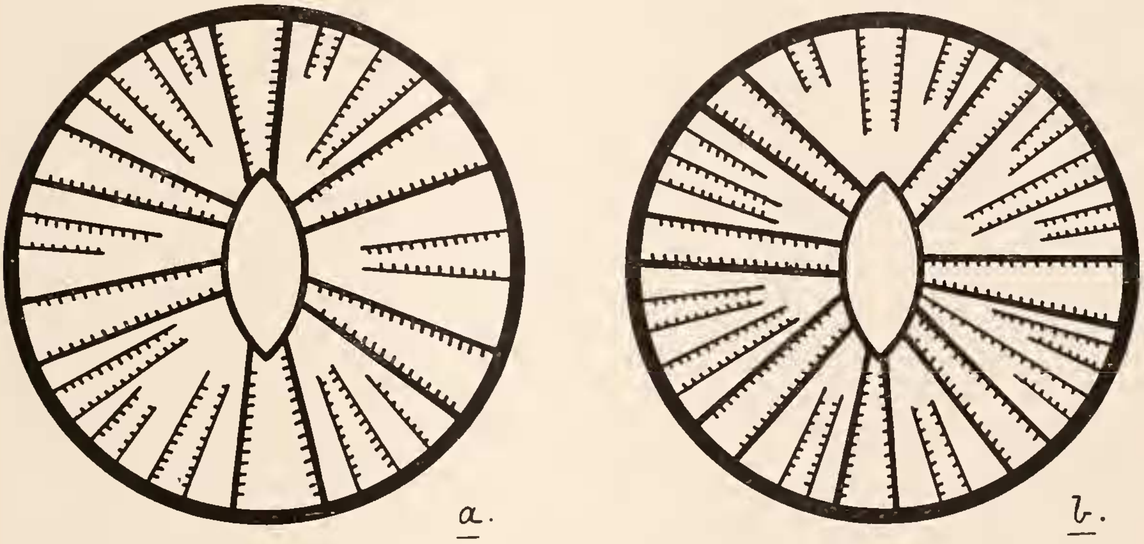

FIG. 5.

Isophyllia dipsacea.—Diagrammatic representation of the mesenteries in two polyps. The hexameral plan is departed from, the cyclic character is irregular, and no directives occur.

The mesenterial development of *Manicina* has been traced from polyps with only one oral aperture to small colonies with four stomodæal systems (p. 503, *et seq.*), and similar early stages have been followed in *Favia* (p. 508, *et seq.*). It is found that in simple polyps with only one oral aperture the hexameral cyclical character of the mesenteries is as regular as in any other sexually-produced polyp, or in adult polyps where columnar budding predominates; two pairs of directives also occur. It is only after fission has been established that irregularities begin to appear, and the hexameral plan is altogether lost. The subject of polypal fission is fully described, and from the manner in which the process takes place it can be easily understood how the above mesenterial irregularities come to be established.

It may therefore be taken as a general rule among corals reproducing by fission, that whether they give rise to distinct polyps, or form meandering systems, their mesenteries tend to lose the hexameral cyclical arrangement characteristic of the earliest stages, and probably never more than two primary pairs of directives are found in any colony, however large. Where the fission polyps are distinct, a cyclical disposition continues to be more or less recognizable, but where complex meandering systems are formed only a single order, including some developing pairs, can be established.

The results on the mesenterial arrangement in adult coral polyps may be thus summarized: The mesenteries in gemmiferous genera are regularly hexamerous, arranged in one, two, or more alternating cycles, and two pairs of directives are present; fissiparous genera are devoid of any hexameral mesenterial plan, are imperfectly multicyclic or acyclic, and without directives. Only the members of the earlier cycles become inserted on the stomodæum in the former, while apparently any of the pairs may become complete in the latter.

DEVELOPMENT OF PROTOCNEMES.

From the time of the publication of the classic researches of Lacaze-Duthiers (1872-73) onward, numerous embryological studies, upon both Actiniarian and Madreporarian polyps, have demonstrated that the twelve primary mesenteries always arise in bilateral pairs, but in an order which seems to vary somewhat in different species. The results of Lacaze-Duthiers were obtained by observation of the external appearances, apparently without confirmation by means of sections, while the latter has been the method more usually followed in later investigations.

In the Actinian larvæ studied by him, Lacaze-Duthiers found that the first mesenterial pair divided the cœlenteric cavity into two unequal compartments, known as dorsal and ventral. The second pair appeared in the larger or dorsal of the two chambers, cutting off a middle chamber; then within the primary smaller or ventral chamber the third pair was developed. According to Lacaze-Duthiers, the fourth pair appeared between the first and second pairs; but in most subsequent researches, among which are those of H. V. Wilson on the coral *Manicina areolata*, J. P. McMurrich on the Actinian *Rhodactis sancti-Thomæ*, and G. von Koch on *Caryophyllia cyathus*, the fourth pair has been found to appear in the dorsal chamber beyond the second pair, and its members become the dorsal or sulcular directives. The fifth and sixth pairs were found to arise nearly simultaneously within the middle and ventro-lateral chambers on each side.

According to the Hertwigs (1879), the fifth and sixth mesenterial pairs arise in *Adamsia diaphana* on opposite sides of the polyp between the first and second pairs. This has also been confirmed by Boveri (1889). In the light of subsequent results, such a condition must undoubtedly be looked upon as exceptional, having been met with in no other species, while the number of forms in agreement with the relationships given above is continually increasing in the Actiniaria, and is the only sequence yet met with in the Madreporaria. Appellöf (1900), in connection with his studies on the development of *Urticina crassicornis* and *Actinia equina*, discusses at some length the conclusions of Lacaze-Duthiers and later writers with regard to the mesenterial sequence of the primary eight mesenteries. In contradistinction to the successive development which Lacaze-Duthiers describes for *A. equina*, Appellöf found that the first eight mesenteries appeared for the most part simultaneously, and doubts the possibility of the order of appearance being determined by external observation alone without the assistance of sections. Sometimes only the strongly developed ventro-lateral pair of mesenteries would be visible from the outside, while transverse sections would demonstrate four pairs. His results on *Urticina* showed considerable variability in the mesenterial sequence. Reviewing the statements of different Actinological writers with regard to the appearance of the primary mesenteries, Appellöf (p. 55) comes to the conclusion: "Es ist wenigstens auf Basis des vorhandenen Materiales unmöglich eine bestimmte Regel auszufinden."

In comparison with the variable results obtained in the Actiniæ the protocnemic sequence in the Madreporaria appears to be very uniform.

Two most complete series of stages in the development of the protocnemes of Madreporarian polyps are already known, thanks to the labors of Prof. H. V. Wilson and Prof. G. von Koch. The former (1888) has traced their appearance in the West Indian coral, *Manicina areolata*, from the stage in the larva with but one pair of mesenteries to the young polyp with three cycles of mesenteries. His results as to the first cycle conform with those of Lacaze-Duthiers on various Actinian types, the second and fourth pairs being transposed.

G. von Koch (1897) also describes and figures the order of development in *Caryophyllia cyathus*, from the stage with two pairs of mesenteries to the completion of the first cycle. In this species the order of appearance, subsequent development, and union with the stomodæum of the six pairs are in perfect agreement with Wilson's results. The arrangement on the completion of the six pairs represented in von Koch's fig. 1 exactly corresponds with that of the adult *Madrepora* and *Porites*, that is, four pairs are complete and two pairs incomplete.

My own results upon the larvæ of *Manicina areolata*, so far as they go, conform with those of Wilson. Stages with from three to six pairs of mesenteries have been obtained, the last (Pl. XIX, fig. 135), exactly reproducing the conditions of Koch's figure of *Caryophyllia*. The young polyps of *Manicina* remained for a week or two at the *Edwardsia*-stage, the first cycle of septa arising in the meantime. (See also p. 503.)

The various stages secured in the course of the development of *Favia fragum* serve to supplement the results of Wilson and von Koch on the two corals mentioned (Pls. XIII–XV, and p. 508). The earliest stage (fig. 112) is from non-extruded larvæ obtained from a decalcified colony. Three pairs of mesenteries are present, but only one of the pairs is yet complete, and this divides the cœlenteric cavity into two unequal chambers. In the larger or dorsal chamber a second pair of mesenteries occurs, the members of which, although incomplete, bear rudimentary mesenterial filaments. In the smaller ventral chamber the merest rudiments of another mesenterial pair are also seen. The middle pair, as is generally the case in Actiniarian and Madreporarian larvæ, extends almost the whole length of the cavity, the filaments being strongly developed all the way. The dorsal pair terminates some distance in advance of the aboral end, while the ventral pair has a very restricted course, disappearing vertically before the inner end of the stomodæum is reached, and centripetally never extending beyond the endodermal layer. Clearly, from the proportional extent of their development, both radially and vertically, the mesenteries have not appeared simultaneously, but represent the first, second, and third bilateral pairs in the sequence.

Sections of *Favia* larvæ which had been extruded for six hours reveal the next stage (fig. 113). Two pairs of mesenteries are here united with the stomodæum, and, by comparison with the previous figure, the additional complete pair is evidently the dorsal—the second in the mesenterial sequence. The ventral pair is scarcely better developed than in the former polyp, but in sections immediately below the stomodæum a new pair—the fourth—has appeared at the other extremity of the polyp, and dorsal to the second pair. A few sections below this are found the rudiments of another pair, situated between the first and second pairs (fig. 114). These represent the fifth pair in the mesenterial order and traverse only a few sections. As yet there are no indications of a corresponding pair between the first and third pairs.

Sections of another larva extruded at the same time present the conditions represented in fig. 115. The first three pairs now extend as far as the stomodæum, though the third pair ceases its connection in advance of the others. The fourth pair is more strongly developed, and rudiments of the fifth pair also occur at the stomodæal level, but are stronger below, where also an additional pair—the sixth, situated between first and third, is apparent (fig. 116). Incipient mesenterial filaments are present on the members of the third pair, while on the second pair they are fully developed, but do not extend so far as on the first pair.

Finally, in larvæ which had just settled, four mesenterial pairs have become complete, and the fifth and sixth pairs are well developed in the upper part of the column, but remain free from the stomodæum (fig. 105). All the complete pairs are provided with mesenterial filaments.

The series presented thus demonstrates that in regard to their proportional growth, both vertically and radially, the time of union with the stomodæum, and the appearance of the mesenterial filaments, a definite bilateral sequence is followed in the development of the protocnemes. The result is as follows:

(*a*) The first pair becomes the dorsal moiety of the ventro-lateral pair of mesenteries on each side of the adult polyp.

(*b*) The second pair becomes the dorsal moiety of the dorso-lateral pairs of the adult polyp.

(*c*) The third pair forms the ventral directives.

(*d*) The fourth pair constitutes the dorsal directives.

(*e*) The fifth pair becomes the ventral moiety of the dorso-lateral pair of mesenteries on each side of the polyp.

(*f*) The sixth pair becomes the ventral moiety of the ventro-lateral pairs of mesenteries on each side of the polyp.

Among the many larvæ sectionized very few irregularities have been met with. Sometimes one member of a pair will appear in advance of the other; in one larva only five complete mesenteries occurred, one member of the third pair having lagged behind. A young polyp settled for some time still presented only three complete pairs along with three incomplete pairs.

Although none of the other larvæ which have been studied present so complete a series as *F. fragum*, yet all the evidence from them goes to support the sequence just established. They each represent *Favia* at one or other of its developmental phases. Newly-hatched larvæ of *Isophyllia dipsacea* contain three pairs of mesenteries, the pairs differing greatly in the extent of their development (Pls. XVII, XVIII). The middle pair again extends nearly the whole length of the larva, and bears filaments which are strongly developed, especially at their lower extremity. Of the two smaller pairs, one is very rudimentary, while the other extends a short distance below the stomodæum. The stage very closely corresponds with that in the earliest available larva of *F. fragum* (fig. 112).

The non-extruded larvæ of *Porites clavaria* also reveal a phase with three pairs of mesenteries, while the mature polyps never get beyond the mesenterial stage with four pairs complete and two pairs incomplete—a stage represented by *F. fragum* at the time of fixation.

The larvæ of *Agaricia agaricites* on extrusion already possess the six pairs of primary mesenteries, all extending nearly the full length of the larva, but only the first four pairs are united with the stomodæum (Pl. XXV). Below the stomodæal region all the twelve mesenteries also bear well-developed mesenterial filaments. In this species, then, the stage reached by the larva on hatching is directly comparable with that in *Favia fragum*, *Manicina areolata*, and *Caryophyllia cyathus* at or about the time of fixation, as well as with the adult polyps of *Porites* and *Madrepora*.

The earliest larvæ of *Siderastræa radians* sectionized reveal eight mesenteries arranged in four bilateral pairs. The two lateral pairs, representing the first and second in the sequence, are united with the stomodæum, while the dorsal and ventral axial pairs, representing the directives, are free. Of the two directive pairs, the ventral pair (III) is slightly larger than the dorsal pair (IV), and in larva a little older the former becomes united with the stomodæm, while the latter is still free. In larvæ of about this age the fifth and sixth pairs make their appearance, and the dorsal directives uniting with the stomodæum the larva has reached the *Edwardsia*-stage of mesenterial development. At about this stage the larva undergoes fixation. Filaments do not appear on any of the mesenteries until their connection with the stomodæum has been fully established, but in most other species they are formed while the mesentery is still free.

The order of appearance and subsequent development of the primary twelve mesenteries, within the sexually produced larvæ and young polyps of the Madreporaria, thus appears to be very uniform, for no exception to the sequence first established by Wilson and von Koch has yet occurred. In the extent of its development, and also in its strong mesenterial filaments, the first pair to arise usually assumes predominance, and retains it until most of the other mesenteries become fully established. While the second and third pairs are scarcely apparent the first pair may have grown nearly the full length of the larva, each member tipped with the mesenterial filament all the way. The second, third, and fourth pairs follow one another in regular succession, uniting with the stomodæum in the order of their appearance.

In most Actinological studies the fifth and sixth pairs are stated to arise simultaneously, and H. V. Wilson observes the same for *Manicina*. Though such may often be the case, instances occur in which one pair appears in advance of the other, and where the same pair becomes united with the stomodæum before the other. Young polyps of a *Sagartia* from Beaufort, for which I am indebted to Dr. C. Grave, all show in section that the bilateral pair between the first and second Edwardsian pairs becomes inserted on the stomodæum in advance of the pair between the first and third Edwardsian pairs. Another such instance occurs in the bud polyp of *Cladocora arbuscula*, represented in transverse section on Pl. VIII, fig. 60. The polyp was preserved in a fully distended condition, the disk protruding in a cone-like manner above the zone of tentacles.

Transverse sections through the discal cone reveal five pairs of complete mesenteries, without any indications of others. The musculature is yet too feebly developed to allow of the paired character of the mesenteries being established by this means alone, but the larger interspaces and the examination of lower sections prove that the enumeration added is correct. In addition to the four Edwardsian mesenteries, the bilateral pair between the first and second pairs is complete, while the pair between the first and third, to be seen in the sections below, is still incomplete. In sections through the actual column wall, below the stomodæal region, the six pairs of protocnemes are equal in radial length, and six alternating pairs of metacnemes occur, the sulcar members a little in advance of the sulcular. In this instance the fifth pair is again complete before the sixth, and the first cycle of metacnemes is established before all the protocnemes are united with the stomodæum. In the bud of *Astrangia*, represented on p. 460, fig. 8*a*, the fifth mesentery on the right side is completed before the one on the left side.

In the section of the larva of *Favia fragum*, represented in fig. 114, the pair between the first and second Edwardsian pairs is already represented on the larval wall, some distance below the stomodæum, by small mesoglœal enlargements, but no trace of any such enlargement yet occurs between pairs I and III, where the sixth pair will be situated (*cf.* fig. 116).

From these examples there can be no doubt that though the fifth and sixth pairs may at times appear simultaneously, yet at other times an interval occurs. The pair of mesenteries between the first and second protocnemic pairs is to be regarded as the fifth in the sequence, and the pair between the first and third as the sixth or last in the development of the protocnemes. The enumeration of these two pairs in H. V. Wilson's figures of the mesenteries in an attached larva of *Manicina* (Pl. V, fig. 39) should therefore be reversed.

In all the instances yet referred to, the fifth and sixth mesenterial pairs remain free from the stomodæum, and in numerous cases it has been found that this condition is retained for a very lengthened period. In young polyps of *S. radians* completion was not attained within the course of four months, though the second cycle of mesenteries had appeared in the meantime. Likewise in the young polyp of *F. fragum*, with four pairs of metacnemes, they are still free (Pl. XIV, fig. 109). All coral larvæ appear to settle at or about the *Edwardsia*-stage, and the septa then begin to make their appearance.

No important resting stage, in the appearance of the protocnemes, seems to be indicated in any of the investigations yet conducted on the Madreporaria, though the comparatively strong development of the first pair must not be overlooked. With this possible exception, the development from the first to the sixth pair progresses with uninterrupted regularity, and the same may be said of the further growth of the first four pairs, as concerns their union with the stomodæum, but a prolonged interval separates the further development of the fifth and sixth pairs. Lacaze-Duthiers and others have endeavored to establish several resting stages in the appearance of the six pairs of primary mesenteries of the Actiniaria, but the Madreporaria afford little support for such.

The incompletion of the fifth and sixth protocnemic pairs is permanent in certain Zoantharia, and therefore this condition can not necessarily be looked upon as a developmental resting stage in the sense of Lacaze-Duthiers. Wherever these pairs appear in the Actinian family Edwardsidæ, they remain free from the stomodæum, and the same relationship holds for *Gonactinia*, etc. Throughout the Zoantheæ the fifth pair remains incomplete, and the sixth pair becomes complete only in macrotypic members of the group. In the West Indian *Aiptasia annulata* (Les.). I have found the pairs to remain free for the most part, although the second, third, and fourth orders of mesenteries were fully developed. They remain permanently free in *Madrepora* and *Porites*, even when an increase beyond the usual twelve takes place. Numerous other instances may be cited, all tending to show that some significance attaches to the incompletion of the fifth and sixth protocnemic pairs, as compared with the completion of the other four bilateral pairs. It is not merely a lagging behind in growth due to their later appearance.

My studies lead me to believe that the earliest corals and Actinians were characterized by anisocnemic pairs (excepting the directives), as compared with the isocnemic pairs of later corals and Actinians. To-day, the former condition is retained in the Zoanthids, and in *Porites* and

Madrepora, and as regards the protocnemes it persists for a long time in the growth of all others. The union with the stomodæum of the fifth and sixth protocnemic pairs is assumed after a time by forms characterized by cycles of isocnemic mesenteries; but they remain incomplete in Actinians and corals (Zoanthids, *Porites*, *Madrepora*) characterized by anisocnemic pairs throughout. Perhaps an earlier phylogenetic stage is represented by the Cerianthids and Alcyonarians, in which the incomplete moieties altogether fail to appear.

Much difference is apparent as regards the position at which the mesenteries first make their appearance. The first two or three pairs seem to arise in the angle between the stomodæal wall and the outer wall of the larva, and then to grow in both directions—that is, down the stomodæal wall and the larval body wall, the latter extension being the more rapid. This is very clearly shown in the figure of the living larva of *Isophyllia*, and in the sections through the oral region (Pl. XVII). While the members of the middle pair extend all the way down the stomodæal wall, and nearly as far as the aboral pole of the larva, the two smaller pairs pass scarcely at all down the stomodæum, and only for a short distance along the larval wall. The three first mesenterial pairs in *Favia* probably arise in the same circumoral position, but the fourth pair is first apparent on the larval wall a little below the stomodæum (Pls. XIV, XV), and the fifth and sixth pairs arise still farther down.

Early bud polyps of *Madrepora* also illustrate the same relationship (Pl. III). Here the four primary mesenterial pairs are seen in the angle between the outer wall of the bud and the stomodæal wall. They extend the whole length of the stomodæum, and for some distance along the outer cœnosarcal wall. On the other hand, the rudiments of the fifth and sixth pairs are first seen on the outer wall, some distance removed from the oral aperture.

Probably in most Actiniaria and Madreporaria the fourth, fifth, and sixth protocnemic pairs arise independently of the stomodæum, and some way from the oral pole. When the appearance of the tentacles has established the topographical regions of disk and column wall, the metacnemic pairs are also found to arise somewhere on the latter, usually nearer the oral than the aboral extremity. Only later do they grow upward, and then inwardly along the discal wall, and in most cases ultimately reach the stomodæum and extend down it.

A marked distinction may thus be established in the place of origin of the different mesenterial pairs, the distance from the oral apertures varying with the relative age of the mesenteries; the earliest pairs arise circumorally, the later pairs are some distance removed. This further supports the contention that the Anthozoa are not primitively cyclical forms, but suggest an ancestry in which the organs appeared bilaterally, in an antero-posterior succession.

Several early stages, obtained in the development of bud polyps, suggest that in the asexual method of increase there is the closest agreement in the order of appearance of the mesenteries with that above described for the sexually produced polyps. The earliest stages have not been secured, and the evidence is therefore not so complete as in the larvæ. The youngest bud is one of *Cladocora arbuscula*, in which eight protocnemes are already present, all united with the stomodæum. Shortly below the stomodæum only four mesenteries remain, and bear mesenterial filaments; then two of these disappear, and the remaining couple are continued much farther, and bear filaments almost to their termination. The musculature at this stage is too weak to permit of the actual arrangement in pairs being determined by means of it, but from the greater length of one pair of mesenteries, and the stronger development of its filaments, it may reasonably be assumed that it represents the first pair of mesenteries, and that the order of disappearance of the others indicates their successive origin.

In other buds of *Cladocora* examined, all the protocnemes are already developed, the Edwardsian mesenteries complete, and the fifth and sixth pairs incomplete, just as in larvæ at or about the time of fixation (Pl. VIII, fig. 61). Buds of *Solenastræa* have also been secured, in which only four pairs of mesenteries are complete and bear mesenterial filaments, while the two incomplete pairs are without filaments, and disappear in advance of the other mesenteries (Pls. XI and XII). The bud polyp of *Astrangia*, whose mesenterial plan is represented on p. 460, indicates a somewhat later stage. In the very early bud of *Madrepora*, already referred to, all the protocnemes are present, but their relative sizes are in conformity with those of the buds of *Cladocora* and *Solenastræa*, and may indicate a like successive origin.

Summarizing, we find: (1) That the twelve protocnemes arise as six bilateral pairs in a definite sequence, which is probably the same throughout the Madreporaria, and conforms with that characteristic of most Actiniaria. (2) The first two or three pairs arise at the angle between the stomodæum and the larval wall, while the later mesenteries first appear on the column wall, some distance from the oral aperture. (3) Two pairs of directives are always present, formed from the third and fourth pairs of the mesenterial sequence. (4) The first four pairs unite with the stomodæum in the order of their appearance (*Edwardsia*-stage), and a long interval elapses before the fifth and sixth pairs become complete; the fifth pair may develop somewhat in advance of the sixth pair. In some cases the fifth and sixth pairs are permanently incomplete. (5) The development of the protocnemes in asexually produced buds is in close agreement with that of sexually produced polyps.

FIRST CYCLE OF METACNEMES.

While much attention has been given to the order of appearance of the six pairs of protocnemes in the Madreporaria and Actiniaria, comparatively few observations have been recorded with regard to the order of development of the pairs of metacnemes. For the Madreporaria, the establishment of the latter becomes a matter of great importance, seeing that upon it is dependent the order of appearance of the septa, a question already much discussed by students of the hard part of corals, but with varying results.

The transition from the protocnemic to the metacnemic stage of Anthozoan development is one of the greatest morphological significance. Lacaze-Duthiers (1872) was the first to realize this in the Actiniæ, and in his résumé of the development of *Actinia equina* (p. 362) he writes:

"Le nombre, la grandeur, la position et la symmetrie des parties ne sont pas determines par les memes lois à toutes les epoques. Ainsi la loi qui préside à la multiplication des parties depuis l'origine jusqu' au nombre douze, n'est pas la même que celle qui régit la multiplication après que ce chiffre est atteint."

As regards sexually produced coral polyps, no previous accounts of the actual order of appearance followed by the metacnemes are available. The embryological observations of Lacaze-Duthiers, von Koch, and Wilson, so far as concerns the polyps themselves, practically cease with the protocnemic stage. Wilson describes the mesenterial condition in young polyps of *Manicina*, but gives no account of the sequence according to which the stages have been reached.

I have been fortunate in rearing young polyps of *Siderastræa radians* as far as the completion of the first cycle of metacnemes, and the various stages in the appearance of the latter have been obtained. Full details will be published later, but the diagrammatic figs. 6 (*a–e*) indicate the actual results. The polyps at fixation contained only the six pairs of protocnemes, as usual, four pairs complete and two pairs incomplete. The fact that the protocnemes retain this proportional development enables the dorsal and ventral, or sulcular and sulcar aspects, to be determined. The polyps remained thus for about a month, the first and second cycles of tentacles appearing in the meantime; then, in the largest specimens, a mesenterial pair was observed within the dorsal exocœle on each side, situated toward the aboral region of the column. A few days afterwards, a similar mesenterial pair appeared within each of the middle exocœles, the dorsal pairs at the same time extending higher up the column. Later, a mesenterial pair was formed within each of the ventral exocœles; so that six new isocnemic pairs were now present, diminishing in vertical and radial length from the dorsal to the ventral side of the polyp, according to their order of appearance. The fifth and sixth protocnemic pairs remained incomplete throughout.

The six unilateral pairs of mesenteries, of three different sizes, continued their growth *pari passu* with that of the polyps as a whole, and when the latter were about three months old became nearly equal in size, constituting a distinct second cycle. In time, the mesenteries, growing both upward and downward, extended the full length of the column and partly across the disk, but in no instance did they stretch wholly across, and become united with the stomodæum. Subsequent examination, by means of sections, showed that in each pair the retractor muscles were disposed on the faces turned toward each other, thus resembling the unilateral pairs of the first cycle.

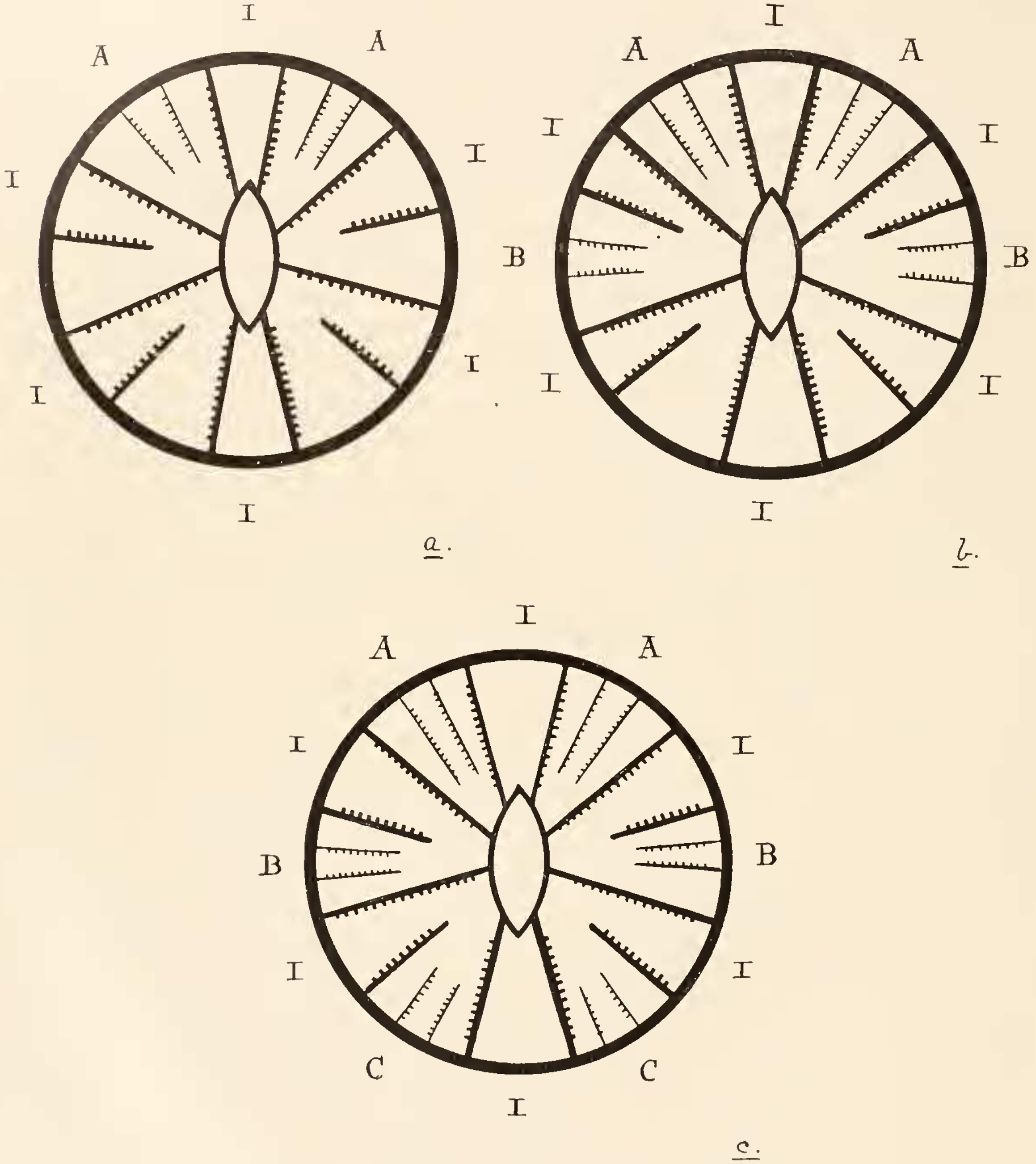

Fig. 6.

Siderastræa radians.—Three diagrammatic figures illustrating the order of appearance of the first cycle of metacnemes in larval polyps. The Roman numerals I are opposite the protocnemic pairs, and the letters A–C indicate the succession of the metacnemes.

While the actual mode of appearance of the mesenteries could be thus followed step by step in *Siderastræa*, young polyps of *Favia fragum* were obtained with the mesenterial conditions shown on pp. 509, 510, and from these certain conclusions are warranted. Four pairs of second-cycle mesenteries are present in fig. 15*e*, in addition to the six pairs of protocnemes. Of the four metacnemic pairs, the two larger are situated within the dorsal or sulcular exocœle on each side of the polyp, and the two smaller pairs are within the middle exocœle on each side (see also, Pl. XIV, fig. 109).

In addition to these two instances, a number of early mesenterial stages have been secured from young buds, and there is little doubt that the process of metacnemic development in these is exactly the same as that followed by polyps with direct larval predecessors.

Fig. 86, on Pl. XII, represents a transverse section through the stomodæal region of an expanded bud of *Solenastræa*. The protocnemes are in the *Edwardsia*-stage of development, and within each of the dorsal or sulcular exocœles a pair of metacnemes has appeared. Sections of the same bud, taken a little below the inner termination of the stomodæum, reveal, in addition, a rudimentary pair of metacnemes within the middle exocœle on the right side, though no trace of new mesenteries appears in the left middle exocœle; the sulcular pairs are also much further developed than in the upper region, and are much larger than the single middle pair (fig. 87).

The stomodæal region of another bud of *Solenastræa*, somewhat younger than the former, is represented on Pl. XI, fig. 82. Of the protocnemes, four pairs again are complete and two pairs incomplete. In this instance the first two pairs of metacnemes are very rudimentary, and appear within the middle lateral exocœles, not as before, within the sulcular exocœles. The new pairs are slightly better developed in sections somewhat lower, but no dorsal or ventral pairs were encountered.

In later buds of *Solenastræa* six pairs of metacnemes occur, a pair within each of the primary exocœles, and these exhibit a developmental succession from the sulcular (dorsal, axial) aspect to the sulcar (ventral, abaxial). In older buds all the pairs are equal in size, forming a regular hexameral second cycle, and this is the adult condition of most of the polyps in a colony (fig. 81).

The diagrammatic representation of the mesenteries of a young polyp of *Astrangia solitaria* on p. 460, also indicates a like dorso-ventral succession for the second order of mesenteries in this species.

Buds of *Cladocora arbuscula* reveal somewhat similar conditions in the appearance of the metacnemes (p. 458). Fig. 61, on Pl. VIII, represents a transverse section through a bud in which two pairs of mesenteries are present, in addition to the six pairs of protocnemes; of the latter only the Edwardsian mesenteries are complete and bear mesenterial filaments. The two pairs of metacnemes (A, A) are very rudimentary, and extend but a short distance down the column wall, and are devoid of mesenterial filaments. The proportional development of the protocnemes enables the dorsal and ventral aspects of the polyps to be determined, and serves to indicate that in *Cladocora* the first metacnemes appear within the ventral or sulcar exocœles, as compared with their dorsal or sulcular origin in *Solenastræa* (Pl. XII). Comparing fig. 87 with fig. 61, the sulcar aspect in both genera is seen to be the outer or abaxial with regard to the rest of the colony, while the sulcular is the inner or axial; therefore, in the two species the metacnemic succession proceeds from opposite aspects.

Pl. VIII, fig. 62, represents a transverse section through a somewhat older bud of *Cladocora*. The specimen is exceptional in that the dorso-lateral pair of protocnemes is missing from the left side, so that the polyp is pentamerous. Five alternating pairs of metacnemes also are present, and their interest in the present connection lies in the fact that they show a marked gradation in the extent of their development, in passing from the outer to the inner aspect. Mesenterial filaments occur on the pairs in the sulco-lateral exocœles, and the longitudinal muscular fibers are also determinable. This latter character is apparent on the metacnemes in the middle lateral exocœles, but no trace of mesenterial filaments occurs. The single pair in the sulculo-lateral exocœle is very rudimentary. The proportional development indicates the same relationship as fig. 61, namely, that the metacnemic sequence is from the abaxial to the axial border of the polyp. At a little later stage the polyps of *Cladocora* consist of six protocnemic pairs, all the members complete, and of six alternating metacnemic pairs, all incomplete and equally developed. Many polyps in a colony are found in this condition.

The manner of appearance of the first cycle of metacnemes in asexually produced coral polyps is thus in closest agreement with that in larval polyps. In both cases they arise as isocnemic pairs within the six primary exocœles, and in bilateral order from one aspect of the polyp to the other, the aspect varying, however, in different species. In *Siderastræa*, *Solenastræa*, *Favia*, and *Astrangia* the succession is from the dorsal to the ventral side, in buds of *Cladocora* from the ventral to the dorsal. The exceptional succession in the latter may be in some way dependent upon the more rapid growth which takes place on the abaxial side of the buds, as compared with the axial. Before it can be regarded as actually characteristic

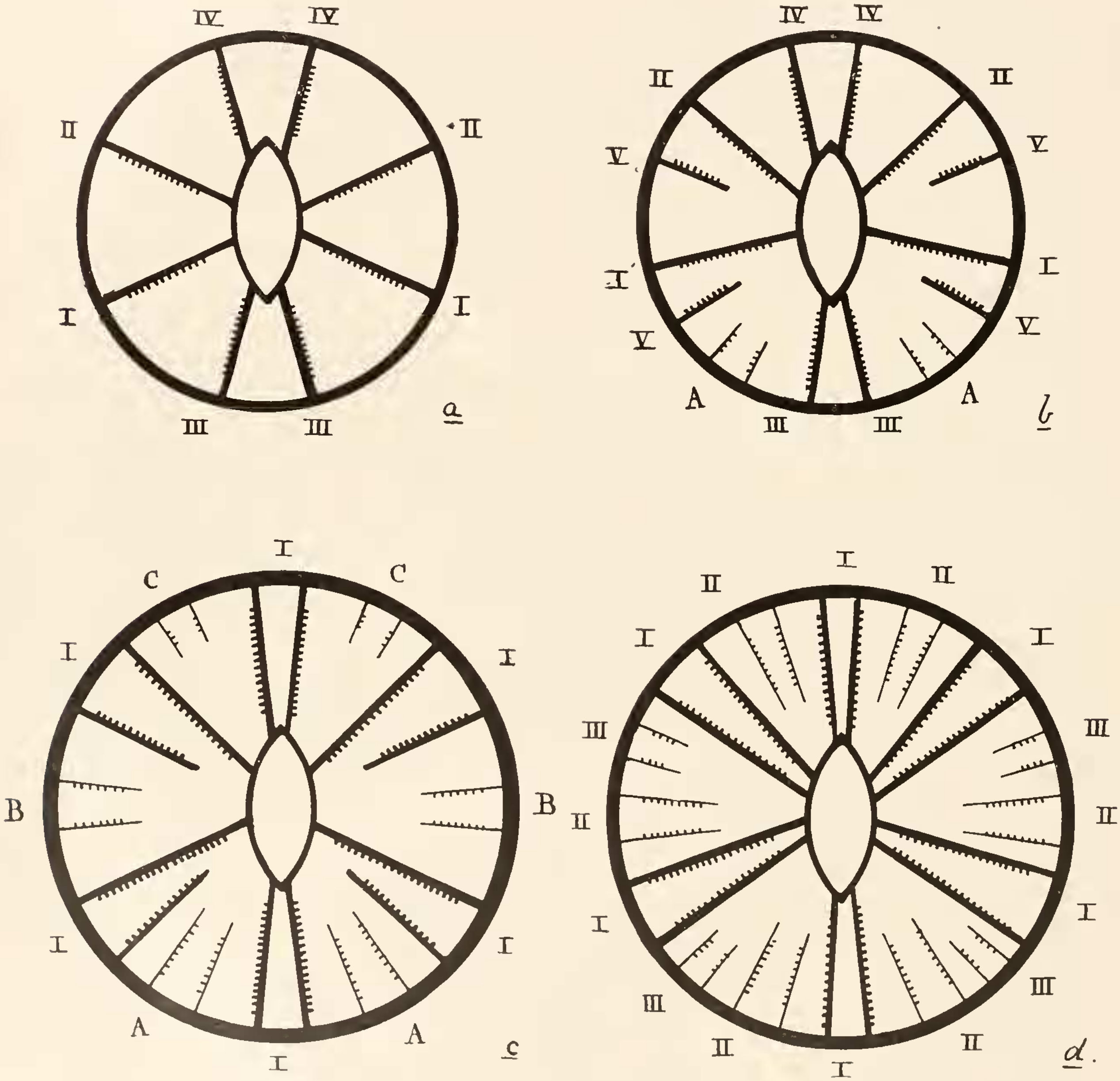

FIG. 7.

Cladocora arbuscula.—Four diagrammatic figures illustrating the order of appearance of the mesenteries in bud polyps (*cf.* Pls. VI–VIII). (In *b* the lower bilateral pair marked V, V, should have been lettered VI, VI.)

of the species, it will be necessary to follow the sequence in polyps reared directly from larvæ, as in the case of *Siderastræa*. Until such is carried out, it may be taken as a general rule that the development of the second order of mesenteries is from the dorsal to the ventral aspect of the polyp; that is, from the anterior to the posterior border.

A wide distinction in their manner of appearance thus separates the members of the second order of mesenteries from those of the first order. The primary mesenteries appear in *bilateral pairs*, in a succession which is first toward one aspect and then toward the other aspect of the polyp, and so on, and only later do they constitute unilateral pairs, in which the musculature is on the faces turned toward each other. With the exception of the directive pairs, the two members of each unilateral pair arise at different times, the dorso-lateral pairs being constituted of mesenteries II and V, and the ventro-lateral pairs of mesenteries I and VI, in the protocnemic sequence; and for a long period the lateral pairs are anisocnemic. The secondary mesenteries also arise in a bilateral manner, but are in *unilateral* (*isocnemic*) *pairs from the beginning*, and in any polyp they are formed in only one succession, from the dorsal to the ventral aspect, alternating with the primary pairs, and situated within the primary exocœles. In mature polyps the secondary mesenteries are all equal, except perhaps in their vertical extent, and are arranged around the polypal wall with perfect hexameral radial symmetry, all traces of their bilateral succession being lost.

Where coral polyps attain considerable size, as in *Orbicella cavernosa* and *Phyllangia americana*, the members of the second order of mesenteries often become united with the stomodæum. In doing so they follow the same antero-posterior succession as that characteristic of their order of appearance in the young polyp (see fig. 9*h*, p. 464).

SECOND CYCLE OF METACNEMES.

The order of appearance of the second cycle of metacnemes, or third order of mesenteries, may now be considered. These, when complete, consist of twelve equal pairs, a pair within each of the exocœles between the protocnemes and the first-cycle metacnemes. The succession has not been followed upon any coral polyp reared directly from the larva, but sufficient evidence is forthcoming from the asexually produced polyps of several species to indicate in a general way the manner in which it is carried out.

Mature polyps of *Cladocora arbuscula* and *Astrangia solitaria* usually contain a certain number of second-order metacnemes, but apparently never the full complement of twelve pairs. It is therefore possible to obtain from these certain intermediate stages in the establishment of the cycle. Pl. VI, fig. 49, represents a section through the stomodæal region of a polyp of *Cladocora* with sixteen pairs of mesenteries. Of these the six complete pairs are protocnemes, the six alternating pairs are first-cycle metacnemes, and the four pairs remaining are the only representatives of the second-cycle metacnemes. The latter are but feebly developed, and without mesenterial filaments. The fact of greatest importance, in connection with the four new pairs of mesenteries, is their restriction to only one exocœle within each of the six primary systems; they are not developed in both the exocœles within the two ventral systems, as considerations of symmetry would suggest. It will be also observed that in each case they occur within the exocœle on the dorsal aspect of the second-order mesenteries (*cf*, p. 458).

The polyps of *Cladocora arbuscula* very rarely pass beyond the stage with sixteen mesenteries, which corresponds externally with thirty-two tentacles. For the further mesenterial sequence therefore other species will be employed.

All the members of an isolated group of eight separate polyps of *Astrangia solitaria* were decalcified and sectionized, and the stage reached in the mesenterial development of each is diagrammatically represented in figs. 8 (*a–g*). Camera lucida drawings of a transverse section from two different individuals are also given on Pls. V and VI, figs. 43, 47. The seven diagrammatic figures reveal that no two polyps in the group were alike in their mesenterial arrangement, so that the series may be taken as affording a fairly complete representation of the order of mesenterial development generally followed in this species.

Fig. 8*a* is taken from the smallest of the polyps. In this instance three members of the protocnemes are still incomplete, and only four pairs of metacnemes have yet appeared, situated within the dorsal and the middle primary exocœles. The sequence of the first-cycle metacnemes is evidently similar to that of the polyps of *Siderastræa* above described (p. 456). In the next largest polyp (fig. 8*b*) the first two cycles of mesenteries are fully established, a pair of metacnemes having appeared within each of the six primary exocœles.

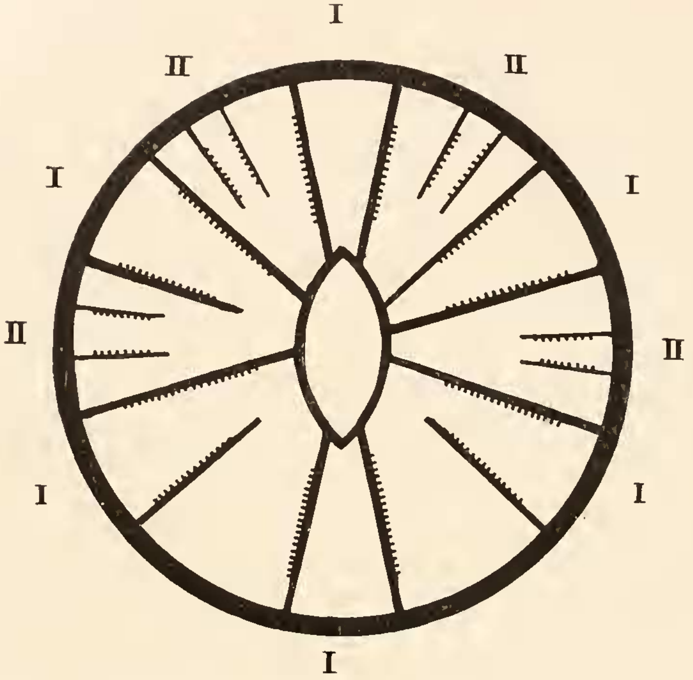

Fig. 8*a*.

Astrangia solitaria.—Fig. 8. Series of diagrammatic figures (*a–g*) illustrating the order of appearance of the mesenteries of the first and second cycles of metacnemes. *a*, Four isocnemic pairs of the first cycle of metacnemes are present (II), while three of the protocnemes are not yet united with the stomodæum.

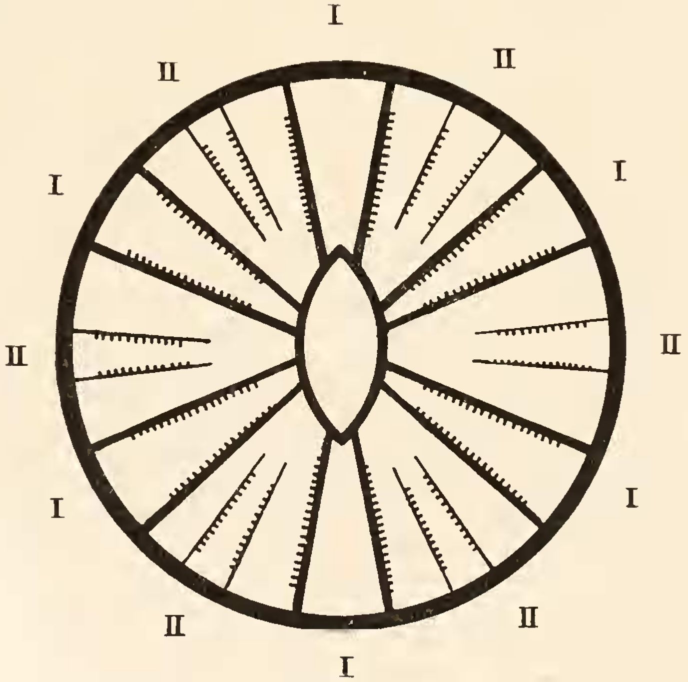

Fig. 8*b*.

Astrangia solitaria.—The protocnemes are all complete, and the six pairs of first-cycle metacnemes have all appeared.

Fig. 8*c* presents the first appearance of the third-cycle mesenteries or second-cycle metacnemes, which are to be especially studied. A new pair of mesenteries has appeared within the exocœle on each side of the dorsal directives and the pair of dorsal second-cycle mesenteries, and a similar pair within the left middle system III.

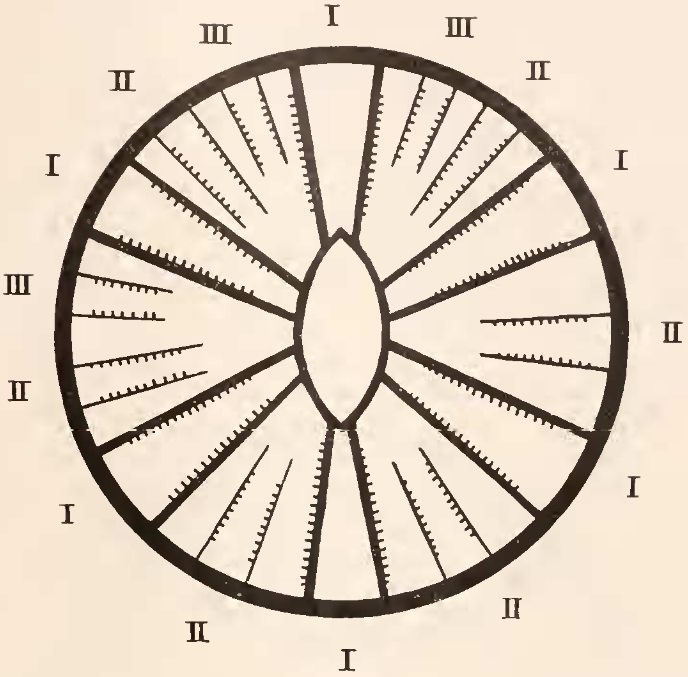

Fig. 8c.
Astrangia solitaria.—Three pairs of second-cycle metacnemes (III) have arisen toward the dorsal aspect of the polyp.

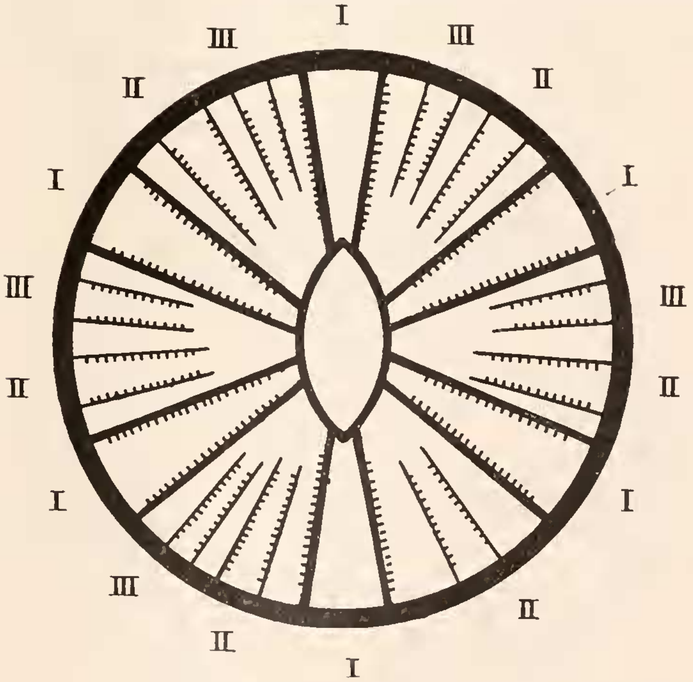

Fig. 8d.
Astrangia solitaria.—Two additional pairs of second-cycle metacnemes have appeared; as yet only a single pair of second-cycle metacnemes is contained within each primary exocœle.

In fig. 8*d* two additional pairs occur, one in the right middle system, and one in the left ventral system. Two other polyps sectionized from another colony exactly correspond with fig. 8*d*.

The polyp from which fig. 8*e* was taken contains a like number of mesenteries, but the right middle system includes only one pair of mesenteries, while the right ventral has two.

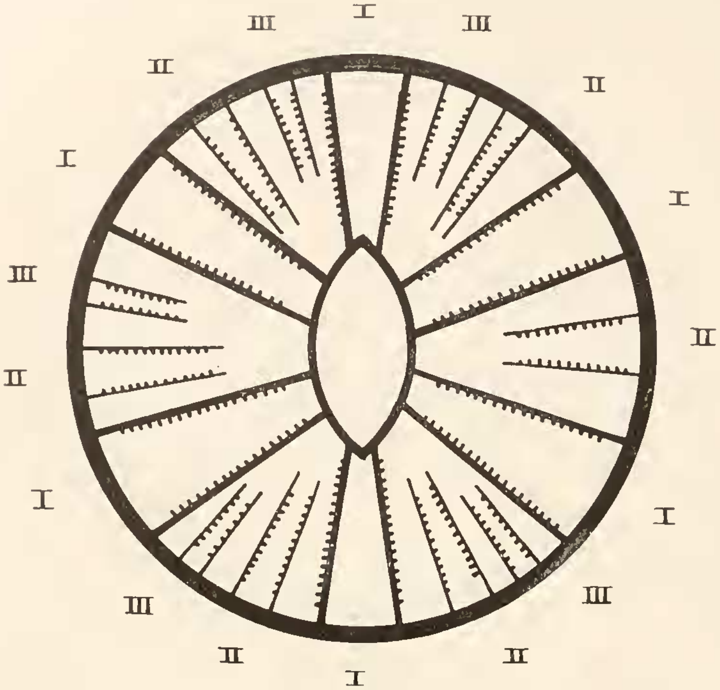

FIG. 8*e*.

Astrangia solitaria.—The development of the mesenteries within the ventral exocœlic chambers is exceptional in that it is in advance of that in the right middle exocœle (*cf*, fig. 47, Pl. VI).

In fig. 8*f*, from another polyp, a third-cycle pair occurs in each of the six primary systems.

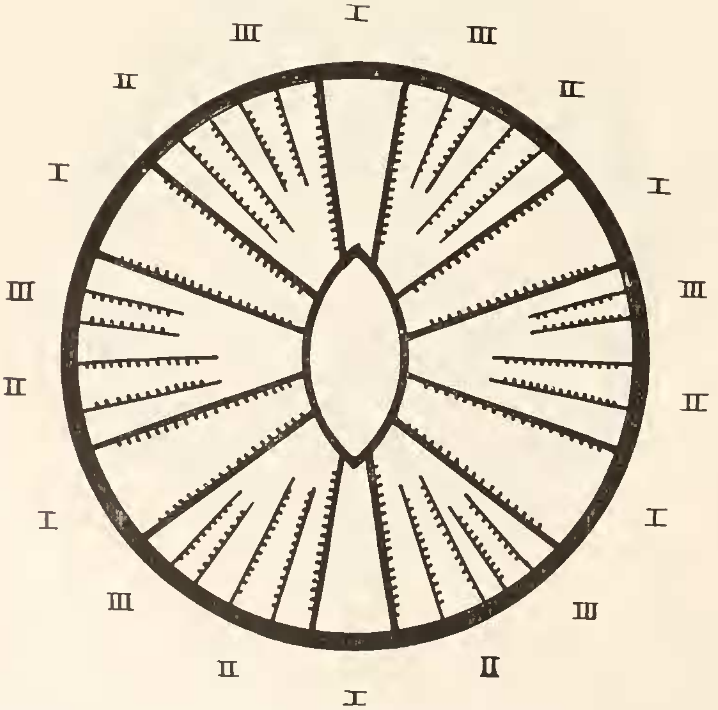

FIG. 8*f*.

Astrangia solitaria.—A pair of second-cycle metacnemes now occurs within each primary exocœle.

So far the series serves to demonstrate the important fact, first suggested by *Cladocora*, that in the establishment of the third order of mesenteries only a single pair first arises within each of the six primary systems, not two pairs—one in the exocœle on each side of the second-cycle pair—as might have been expected. Further, the pairs do not appear simultaneously, any more than do the members of the first and second cycles. They present evidence of a general, though not rigid, succession from one border of the polyp to the other. What this aspect is, whether dorsal or ventral, can not be determined in polyps at this late stage, seeing that the protocnemes are all complete. In isolated polyps apparently no means is available for such an important determination; the relative sizes and vertical extent of the second-cycle mesenteries are of no assistance. The latter are now practically of the same size, and any variation they may present is of very uncertain value. However, as in most species the succession of the second-cycle mesenteries is found to be from the dorsal to the ventral aspect, I have disposed the figures in such a way that they indicate a like succession for the first six members of the third cycle.

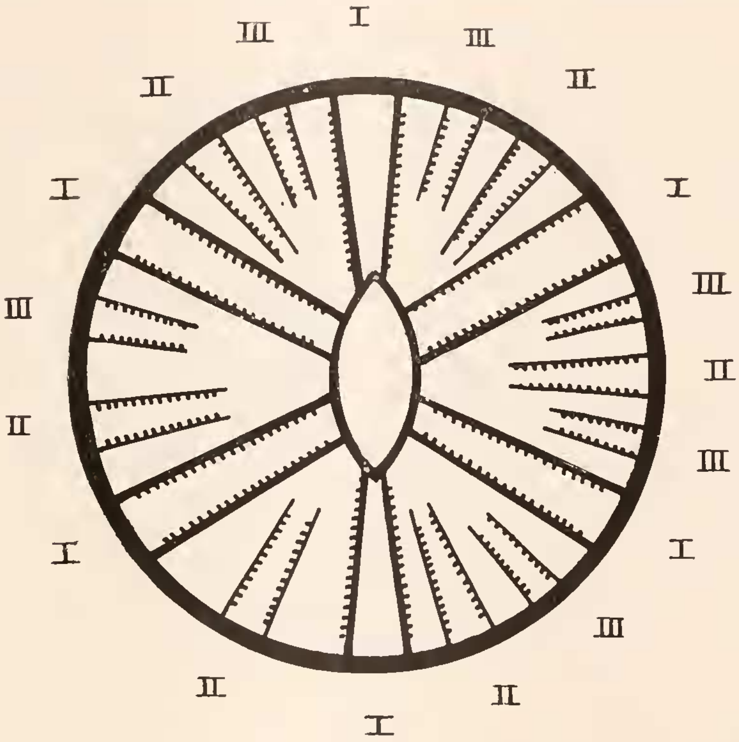

Fig. 8*g*.

Astrangia solitaria.—An additional pair of tertiary mesenteries has appeared within the right middle exocœle (*cf*, fig. 43, Pl. V).

In some instances (fig. 8*c*) the growth is more rapid on one side than on the other, and in fig. 8*e* the right middle pair has lagged behind. In *A. solitaria*, at any rate, a certain amount of individuality in growth is exhibited by each sextant, and mesenteries may appear in one irrespective of the condition in other divisions.

Clearly, in order to complete the third cycle of mesenteries according to the hexameral plan, a second pair of mesenteries must now arise in each of the six primary systems, and within the exocœle on the ventral aspect of each of the second-cycle mesenteries.

Such has already taken place in fig. 8*g* in connection with the right middle system, but a lagging behind occurs in the left ventral system, as only a single mesenterial pair is yet developed.

Polyps of *Astrangia solitaria* rarely exhibit more than seven or eight third-cycle mesenteries; no specimen with the full twelve pairs has been met with. The further stages necessary to complete the third order may, however, be obtained from the larger polyps of the closely allied *Phyllangia americana*.

Fig. 9*h* represents a transverse section through a polyp of *P. americana*, in which ten pairs of mesenteries are complete; six pairs represent the protocnemes, while the other four pairs belong to the second order. The remaining two pairs of secondaries are still incomplete. The full complement of twelve tertiary pairs is present, except for one pair in the dorsal exocœle of the two ventral primary systems. Here, as before, it will be understood that the dorsal and ventral aspects were not actually determinable.

Fig. 9*i*, from a still larger polyp of *Phyllangia*, reveals twelve pairs of complete mesenteries belonging to the first and second orders, and twelve alternating pairs of incomplete mesenteries representing the third order. At the dorsal extremity a few pairs of mesenteries of the fourth order have also appeared. Polyps of *Phyllangia* rarely contain more than this number of mesenteries, so that it has not been possible to follow the method of growth of the fourth order. All that can be asserted from fig. 9*i* is that the mesenteries of the fourth order begin to make their appearance at one extremity of the polyp, which is probably the same as that at which the members of the second and third orders first arise.

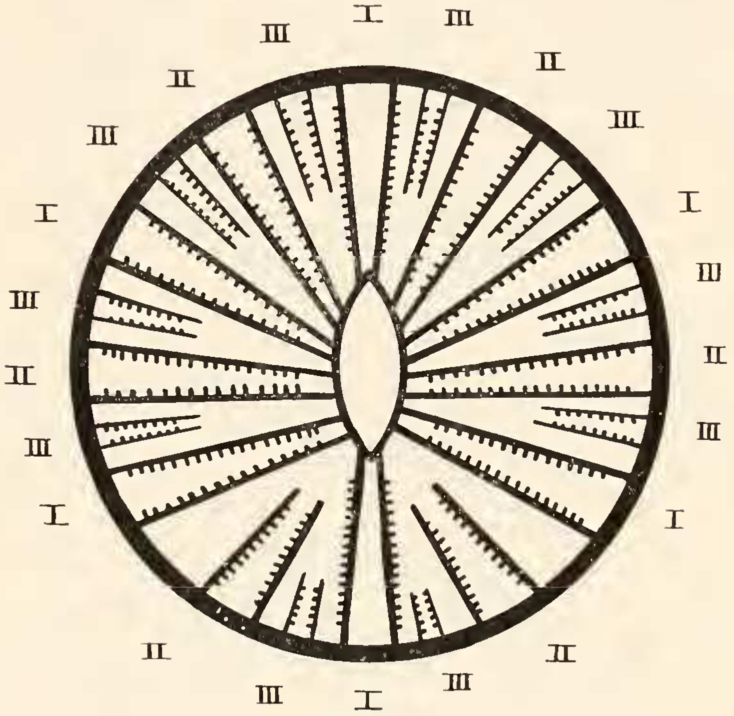

FIG. 9*h*.

Phyllangia americana.—Order of appearance of the metacnemes continued. Other pairs of second-cycle metacnemes (III) are present, and four pairs of the first-cycle metacnemes (II) are now united with the stomodæum. The succession of growth is from the dorsal to the ventral aspect.

The sections of the polyps of *Favia fragum* represented on page 510, and of *Manicina areolata* on page 504, reveal that in these species the order of appearance of the third-cycle mesenteries follows a succession closely comparable with that in *Cladocora*, *Astrangia*, and *Phyllangia*.

The order in which the twelve pairs of tertiary mesenteries are developed may be thus summarized:

The members of the third order of mesenteries arise in successive isocnemic pairs, after the establishment of the secondary mesenteries, within the exocœlic chambers between the pairs of the first and second orders of mesenteries. In a general way, two stages of growth are distinguishable: First, a single pair arises within each of the six primary systems, that is, within only one of the two exocœles, the succession being from one aspect of the polyp to the other; second, another pair appears within each of the remaining exocœlic chambers, the different members of the series of six pairs following the same succession as the first series of six pairs. The regularity is by no means strictly adhered to; growth in one sextant of the polyp may be in advance of growth in another, independently of the general dorso-ventral succession. Part or all of the twelve pairs necessary to complete the order may be characteristic of any species. Ultimately all the tertiary pairs attain the same radial extent, which is less than that of the secondaries.

APPEARANCE OF MESENTERIES IN POLYPS REPRODUCING BY FISSION.

All the examples referred to above, as attaining a cyclical disposition of the mesenteries in the adult polyp, are species reproducing asexually by gemmation. A perfect regularity, as regards the radial length of the mesenteries of the different cycles, obtains in these, exactly as in sexually produced polyps. The organs do not continue their growth indefinitely until reaching the stomodæum; only the members of the first order of six pairs, or, in larger polyps, those of the second order also, become united with the stomodæum. The remaining orders extend for definite radial distances from the body wall, uniform for the members of any one cycle, and in the main characteristic of the species. The adult arrangement has been shown to be otherwise with species in which asexual reproduction by oral fission prevails; and this whether the new polyps become distinct, each with its own tentacular system, or whether they remain incompletely separated, and give rise to meandering tentacular and discal systems (p. 448).

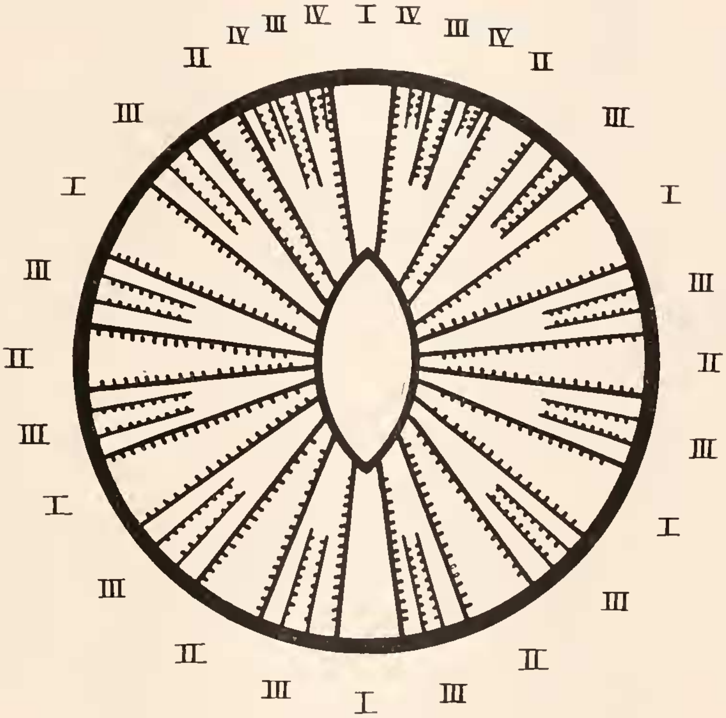

FIG. 97.

Phyllangia americana.—All the secondary mesenteries are now united with the stomodæum, and along with the members of the first order (protocnemes) constitute the first cycle of mesenteries. Four pairs of third-cycle metacnemes (fourth-order mesenteries, IV) have appeared on the dorsal side.

In describing the mesenterial arrangement in the genera *Mæandrina* and *Colpophyllia* (p. 449), it was found that the mesenteries at most are divisible into only complete and incomplete pairs, but that the alternation is by no means constant. Sometimes several complete pairs are found without any intervening incomplete pairs, while, when the latter do occur, they are very variable in the extent of their development. One pair may extend nearly as far as the stomodæum, while another may be merely incipient; further, the complete or incomplete pairs belonging to opposite sides bear no bilateral relation to one another.

In these genera, therefore, the mesenteries manifestly arise in single exocœlic pairs at almost any region of the colony, though more freely in the regions of forward growth. The new pairs, however, do not continue as a separate incomplete cycle, but become larger and larger, and ultimately come into union with the stomodæum, while other new pairs appear in the meantime.

Similar relationships of the mesenteries are also described for *Isophyllia*, *Favia*, *Agaricia*, and others. In transverse sections mesenteries of all sizes are found, representing different stages of growth, but without any regular alternation of small and large pairs; the Roman numerals only approximately indicate any ordinal relationships of the pairs. Here again, one can only assume that the different pairs arise for the most part independently of any cyclic plan, and that each pair continues to increase in size, and may ultimately become complete. If the polyp be in an actively growing condition, fission will again step in, the mesenteries which before were incomplete now become complete, and new pairs continue to arise in the daughter polyps in the same irregular fashion.

When the very regular cyclic arrangement of young polyps of *Manicina areolata* is compared with that after fission is well established (p. 503, *et seq.*), it is seen that the order of appearance of the mesenteries is becoming fundamentally altered. It is manifest that single pairs arise at any point, and grow independently of the others already present, so that in different primary exocœles they may be one, two, three, or even four incomplete pairs.

It may therefore be accepted as a general rule, that in genera reproducing by fission, the mesenteries are not developed according to any regular cyclical sequence, once fission has become established; but they arise as isolated exocœlic pairs, in regions of most forward growth, and each and all the pairs may ultimately become complete. This is more fully illustrated under fission in *Manicina* and *Favia* (p. 502, *et seq*).

INCREASE OF MESENTERIES IN PORITES.

As already mentioned, the tentacles and mesenteries in the genus *Porites* are always twelve in number, and larval in the extent of their development, the Edwardsian mesenteries alone being complete. Very exceptionally polyps are met with in which these organs may be increased to fourteen, sixteen, or even twenty-four, the polyps maintaining a circular form, like that of the ordinary polyp, only larger. Similar numerical increases are likewise occasionally found in the septa of individual corallites. A study of transverse sections of these larger polyps reveals that the increase in the number of mesenteries proceeds in a manner different from any yet described in the Madreporaria. The diagrammatic figures 10 and 11, and the camera drawings on Pl. V (figs. 41, 42), will serve to explain the various sequences followed.

In fig. 41, and 10*a*, is represented a transverse section through the stomodæal region of a polyp in which fourteen mesenteries are present, that is, two beyond the usual number. The twelve primary mesenteries are easily determinable from the arrangement of the retractor muscles, and retain their original condition, that is, four pairs (I–IV) are complete and two pairs (V, VI) are incomplete. Within the sulcar or ventral entocœle, however, another complete pair (A, A) has been added, and the sulcar directives are pushed farther apart. The retractor muscles on the newly added pair are on the faces of the mesenteries turned toward each other, so that each forms with the adjacent directive mesentery a unilateral pair, in which the retractor muscles are on the mesenterial faces turned from one another as in directives proper.

The next stage (fig. 10*b*) obtained is one in which eighteen mesenteries occur: fourteen are in the same condition as in the previous polyp, and the four additional members are situated within the entocœle of the seventh pair. The bilateral pair, B, B, is very rudimentary at this level, but becomes proportionally better developed a short distance below the stomodæal region; each member forms with the adjacent moiety of pair C, C a unilateral, anisocnemic pair, in which the retractor muscles are vis-a-vis. A similar stage is represented in the next figure (fig. 10*c*), except that an unpaired complete mesentery is added within the entocœle of the last bilateral pair C, C. In the polyp from which fig. 10*d* was taken a pair of complete mesenteries occurs, in place of the unpaired member of the previous polyp. Below the stomodæal region, the members of pair D, D are found to belong to the smaller series, corresponding in size with pair B, B.

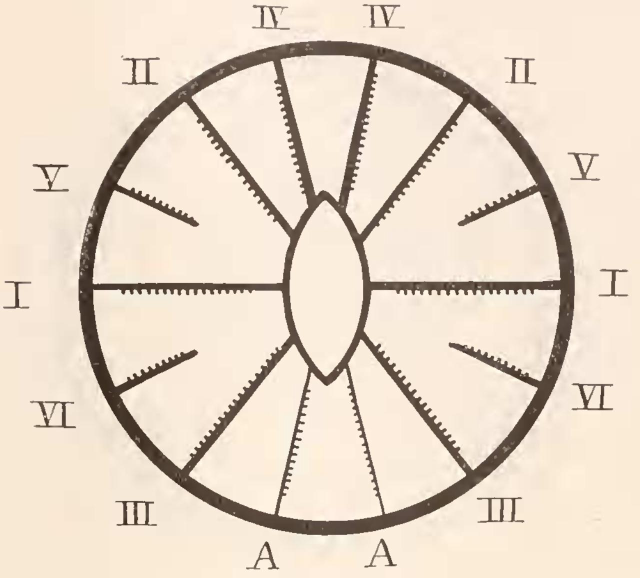

FIG. 10*a*.

Porites.—Fig. 10. Increase of mesenteries beyond the protocnemic stage, as exhibited by various polyps. The six pairs numbered I–VI and represented by thicker lines are the protocnemes. *a*, An additional bilateral complete pair (A, A) occurs within the exocœle of the ventral pair of directives.

All the additions thus far are within the entocœle of the ventral pair of directives, but in fig. 11 the new mesenteries are disposed within the entocœle of the dorsal directives. In 11*a*,

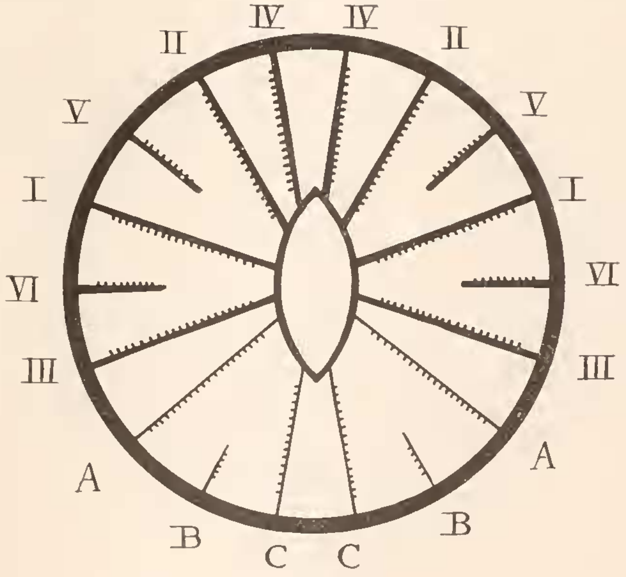

FIG. 10*b*.

Porites.—Two further bilateral pairs have been added; one (B, B) incomplete, and another (C, C) complete. Mesenteries III, A, on each side form unilateral isocnemic pairs, in which the retractor muscles are on the faces of the mesenteries turned away from each other, as in directives; mesenteries B, C, on each side constitute unilateral anisocnemic pairs.

three bilateral pairs are represented, all the members of which are attached to the stomodæum. The retractor muscles are so disposed that, as in the previous instances, the members of the first new pair form with the adjacent members of the primary directives an isocnemic pair of directives on each side, and the moieties of the next two bilateral pairs form a pair on each side, in which the muscles are turned toward each other.

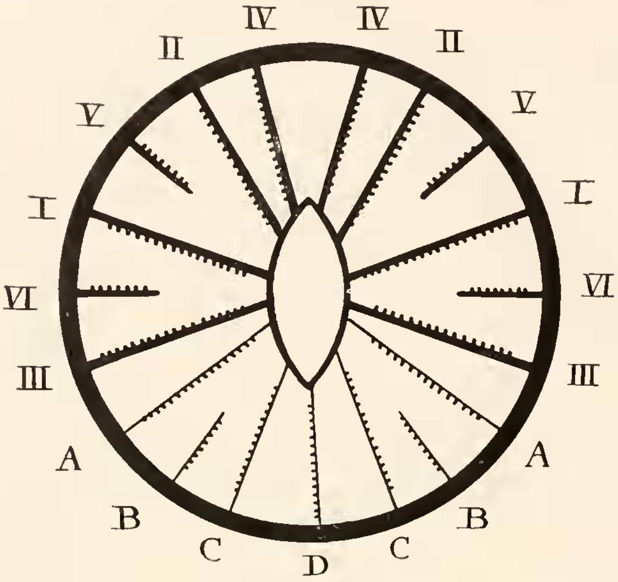

Fig. 10c.

Porites.—A single additional mesentery (D) has appeared without a corresponding member to form a pair.

Fig. 11*b* is the diagrammatic representation of fig. 42, Pl. V, which is taken from a section of an enlarged polyp of *Porites.* The figure of the section will give some idea of the difficulties involved in unraveling the relationships of the various mesenteries to one another. It is only by determining the faces of the mesenteries bearing the retractor muscles, and the proportional sizes of the mesenteries, that the primary and the later mesenteries can be established in their relations to one another. Comparing fig. 11*b* with fig. 42, it is seen how the pairs in the actual section

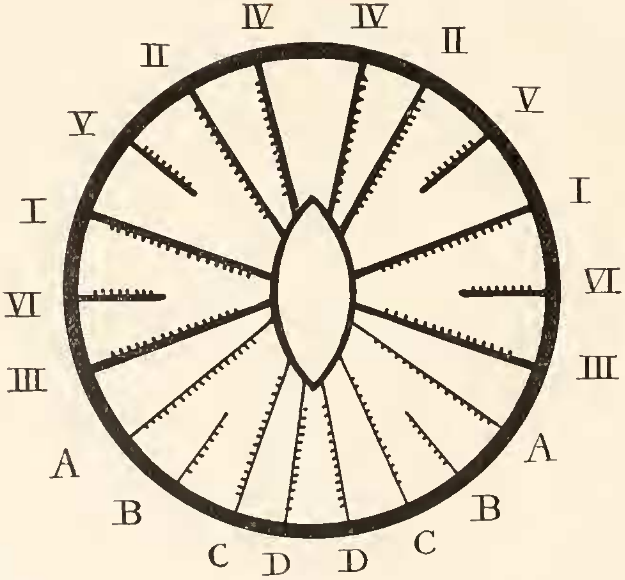

Fig. 10*d*.

Porites.—Four additional bilateral pairs are present. The pair D, D is united with the stomodæum, but below this region is shorter than pair C, C, showing that it belongs to the microcnemic series.

correspond one by one with those in the diagrammatic plan. It is further manifest that no other arrangement of the pairs than that offered would represent the primary mesenteries with the characteristics they present in ordinary polyps. In the region here figured, the dorsal directives belong to the smaller series of mesenteries as well as the new bilateral pair next to them, and as in the previous figure the adjacent moieties of each pair constitute a pair of directives. The next two mesenteries on each side form a unilateral pair in which the ventral moiety is large and the dorsal small.

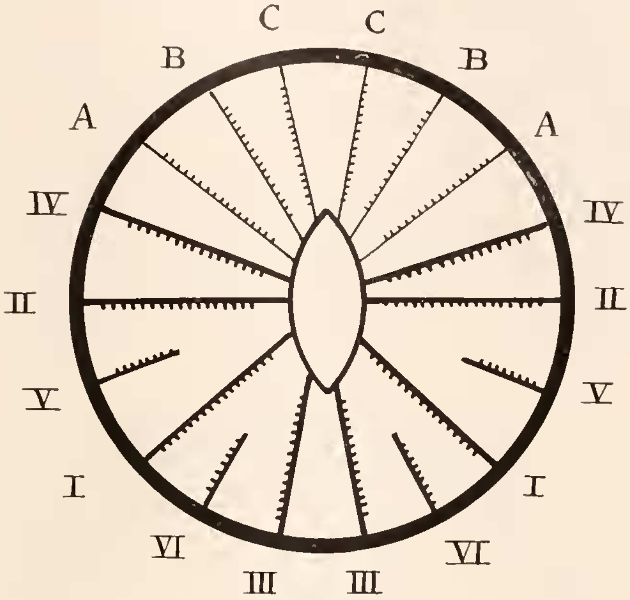

FIG. 11*a*.

Porites.—Fig. 11. Increase of mesenteries continued. All the additions occur within the dorsal directive entocœle. *a*, Three new pairs (A. C) occur, all of which are united within the stomodæum.

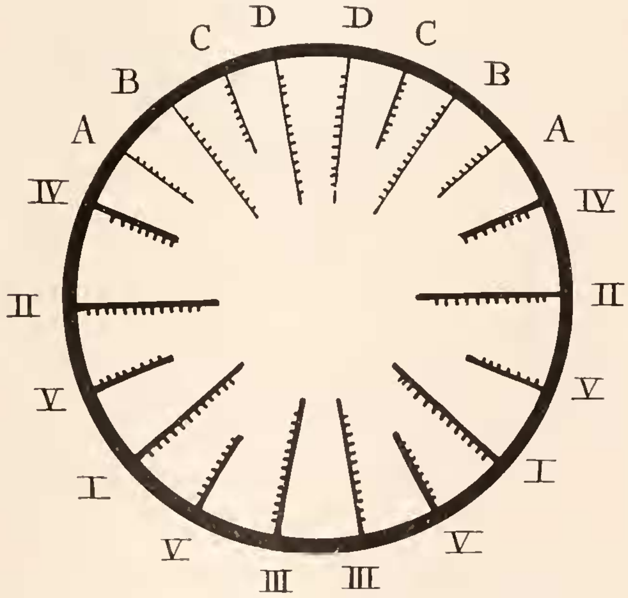

FIG. 11*b*.

Porites.—Section of another polyp, below the stomodæal region. Mesenteries IV, A, on each side constitute microdirectives, and B, C are anisocnemic pairs (cf. Pl. V, fig. 42).

Fig. 11*c* is from a transverse section through the stomodæal region of a polyp in which twenty-four mesenteries are present, arranged in twelve bilateral pairs. The primary dorsal directives (IV, IV) are incomplete at this level, as often happens in ordinary polyps. The unilateral paired arrangement of the six new pairs of mesenteries, as regards the complete and incomplete moieties, is exactly the reverse of that of the primary mesenteries. In the former, the incomplete members have their musculature on faces directed ventralwards, while in the latter it is toward the dorsal aspect. Four isocnemic pairs occur in which the retractor muscles are on the faces turned away from one another (directives), and eight anisocnemic pairs in which the musculature is on the faces turned toward each other.

Of the many living polyps examined, none showed a stage beyond that represented in fig. 11*c*. In one or two instances where twenty-four mesenteries occurred, the stomodæum was found to have undergone fission in the dorso-ventral or directive plane, and with each stomodæal tube were associated six pairs of mesenteries, arranged exactly as in ordinary polyp. Of the six pairs in each fission polyp, three belong to the primary series of mesenteries, and three to the later formed pairs (p. 514).

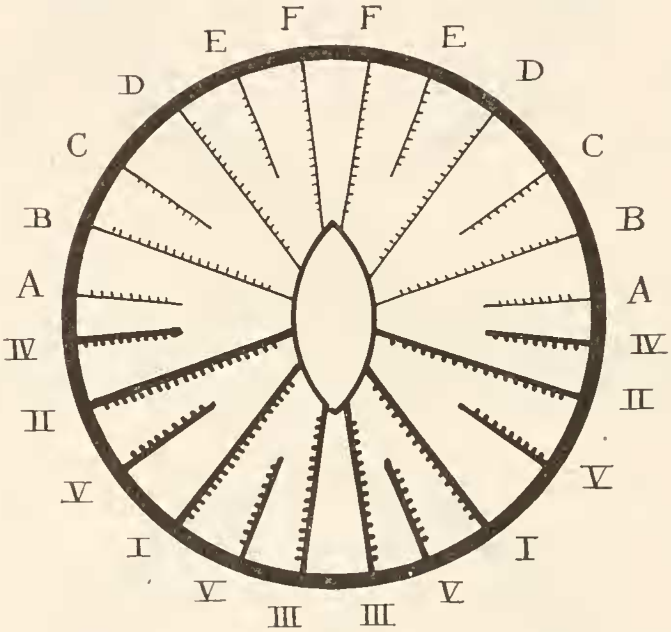

Fig. 11c.

Porites.—Six new mesenterial pairs have appeared, equaling in number and corresponding in arrangement, only in reverse order, with the protocnemes.

The results may be summarized as follows:

1. In *Porites* new mesenteries beyond the primary six pairs are added at only one region, which is within either the dorsal or the ventral directive entocœle.

2. The additional mesenteries appear successively in complete or incomplete bilateral pairs, the latest formed arising within the entocœle of the previously formed pair. Sometimes the moiety of a pair on one side may arise a little in advance of the moiety on the other side.

3. The longitudinal muscles on the mesenteries are so arranged that the members of the first additional pair constitute with the sulcar or sulcular directives, as the case may be, two isocnemic pairs, in which the musculature is on the faces turned away from one another. In the succeeding bilateral pairs, the musculature is alternately on opposite faces, so that the eighth and ninth bilateral pairs on each side form a unilateral pair in which the muscular faces are turned toward each other, and likewise the tenth and eleventh pairs. On the twelfth bilateral pair the retractor muscles are on opposite faces, as in directives proper.

4. Below the stomodæal region both the primary and additional pairs consist of alternately

longer and shorter mesenteries (anisocnemic), with the exception of the directives, which, whether lateral or axial, consist of equal moieties (isocnemic).

5. When the number of mesenteries in a polyp reaches twelve pairs, stomodæal fission may take place, in such a manner that six primary and six new mesenteries are associated with each stomodæum.

A great distinction is thus established between the manner of appearance of the metacnemes in *Porites* and that in other coral polyps. In the former, the additions are shown to take place in bilateral pairs at only one region, and within an entocœle, while in the latter it has been shown that the additions are made in unilateral pairs all round the polyps, within the six primary exocœlic chambers. In *Porites*, the unilateral pairs consist of a larger and a smaller moiety (anisocnemic), without the formation of hexameral cycles, while in other Madreporaria the members of a pair are alike in size throughout (isocnemic), and in the end the different pairs constitute cycles.

Later results suggest that the additions in *Porites* are to be regarded as stages in the process of fissiparous gemmation. (See foot-note, p. 496.)

INCREASE OF MESENTERIES IN MADREPORA.

In a recently published paper,[a] I have fully described the peculiar manner in which the increase of mesenteries beyond the protocnemic stage takes place in *Madrepora*. The process is again alluded to on p. 515, in connection with fission in *Madrepora*, and is illustrated by three diagrammatic figures (fig. 18*a-c*). Fundamentally, the increase takes place in the same manner as in *Porites*, that is, by bilateral pairs, which are disposed within the directive axial entocœle. But in any one polyp of *Madrepora* additions are made at both extremities, whereas, in *Porites*, they are restricted in any one polyp to either the dorsal or the ventral directive entocœle. Six new pairs seem to rise simultaneously in *Madrepora*, as against the successive order in *Porites*; for some time one or two of the pairs may be united with the two stomodæal tubes, without any connection with the column wall.

MESENTERIAL FILAMENTS.

The edges of all the complete mesenteries, after ceasing their connection with the stomodæum, are provided with the Anthozoan structures known as mesenterial or gastric filaments, and likewise the free edge of most of the other mesenteries, which at no time extend transversely so as to reach the stomodæum. In dissected polyps the filaments appear as dense, white, thread-like organs, connected with the mesenteries, usually straight and vertically descending in the upper region, but greatly convoluted below. In the living condition, they are frequently extruded through the mouth and polypal wall, as white coiled threads, along with the portion of the mesentery to which they are attached. They are generally strongly marked off from the rest of the tissues in microscopic preparations, on account of the brightly-staining character of their cellular constituents.

On the incomplete mesenteries, the filaments, as a rule, commence a short distance from the uppermost region of the polyp, and terminate below somewhat in advance of the mesentery; occasionally they are absent from the last cycle of mesenteries, or remain incipient. On the other hand, the filaments are borne by the complete mesenteries only after ceasing their connection with the stomodæum. At first they are straight, but soon become greatly convoluted, on some mesenteries more than on others.

Structurally, the filaments display the same essential characters in all the species examined, and are simpler than the corresponding organs in the majority of Actiniaria. Throughout the Madreporaria, so far as yet known, the actual filament consists of only a single median lobe, in contrast with the trilobed condition of most Actinian filaments. In transverse sections the organs appear as cordate or disk-like expansions of the edge of the mesenteries. In addition to the actual terminal filament, the mesenterial epithelium immediately behind is usually much swollen on each side, and is either sharply rounded off from the rest of the endoderm or passes

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[a] "The Morphology of the Madreporaria.—II. Increase of Mesenteries in *Madrepora* beyond the Protocnemic Stage." Ann. Mag. Nat. Hist., Ser. 7, Vol. X, 1902.

gradually into it. Figs. 14, 39, 44, 45, 57, and 69 will give some idea of the variety of form presented in transverse sections.

Histologically, a filament differs in passing vertically from one region of the polyp to another, and also exhibits a variety of cellular constituents in different parts of the same section. In the complete mesenteries the actual boundary between the stomodæal ectoderm and the mesenterial filament is by no means well defined. As shown on Pl. VI, fig. 51, the deeply-staining ectoderm of the stomodæum, at the termination of the latter, appears to pass around and for some distance along both sides of the mesenteries, and as the latter become free they are capped with the ectoderm. In transverse sections (fig. 57*b*) the filament at first is cordate, the mesoglœa bifurcating and supporting the lateral wings. The anterior and lateral borders of the filament differ in no respect histologically from the stomodæal ectoderm, while the posterior borders are ordinary mesenterial endoderm. The first part of the filament in most corals is of this character, but continues thus for a longer distance in some form (*Cladocora, Astrangia*) than in others. The stage is never represented in the filaments of mesenteries which are unconnected with the stomodæum. It passes gradually into the next stage, which represents the longest part of the filament (fig. 57*c*). The anterior or inner portion of the filament is constituted mostly of narrow nematocysts, clear and granular gland cells, and supporting cells, while laterally and behind the cells become shorter, supporting cells predominate, and the ciliation is stronger than elsewhere. The mesoglœa of the mesentery passes but a short distance into the filament, and there bifurcates, each half being directed forward, horizontally, or backward, and quickly thinning out. Immediately in front of the mesoglœal expansion nervous elements are usually recognizable, and less often muscular fibrils. The latter may also be present along the hinder mesoglœal border, as a continuation of the mesenterial muscle layer (*cf.* also figs. 44, 45, Pl. V.)

Passing to the lower regions of the polyp, the filaments usually become broader in transverse sections, and large, oval, thin-walled nematocysts, with a very distinct spiral thread, are the chief feature. So abundant are the stinging cells that in some cases they make up by far the greater proportion of the whole filament, the supporting cells serving as a kind of matrix (Pl. VII, fig. 58; Pl. XIII, fig. 94)[a].

The swollen mesenterial endoderm, immediately behind the filament, must in no ways be confounded with the two lateral lobes of the trilobed Actinian filament. In these the three lobes are very distinct structures, both as to their form and histology, and each is supported upon a separate mesoglœal axis. The apical part of the middle lobe (Drusenstreif) is mainly glandular in character in the upper region of the polyp, and a few small nematocysts usually occur. On their antero-lateral borders, the two lateral lobes are constituted wholly of ciliated supporting cells, being known as the ciliated bands or Flimmerstreifen. Between the glandular streak and the ciliated bands is found a patch of tissue, which as a rule bears a close resemblance to undifferentiated endodermal epithelium, and has been termed the intermediate streak.

Comparing the coral filament with that of the Actinian, it is manifest that the organ in the former is represented by the middle lobe of the latter, and there is nothing which corresponds morphologically with the lateral lobes. The lateral lobes of coral polyps never contain a separate mesoglœal axis, and histologically they bear the closest resemblance to the ordinary mesoglœal epithelium. In Actinians the lateral ciliated lobes disappear aborally, and also distally on the incomplete mesenteries, while in certain genera (*Corynactis, Rhodactis*) the lateral lobes are altogether wanting, when the filament is essentially like that of the Madreporarian polyp.

Histologically the postero-lateral region of the coral filament, especially in *Madrepora* (p. 474), closely recalls the ciliated streak of anemones, and its strong ciliation also suggests a similar function.

The filaments on the imperfect mesenteries often remain in a rudimentary condition, and afford instructive stages in the development of the organ. The free edge of the mesentery is

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[a] None of the mesenterial filaments examined ever show the nematocysts partly extruded, in the manner described and figured by Bourne for *Fungia* (1893, pl. XXIV, fig. 28), and by Pratt for *Neohelia* (1900, pl. LXIII, fig. 8); but in the polyps of certain Pacific corals I have observed the phenomenon noticed by these authors.

capped by a tissue which stains brightly, and consists mainly of ciliated supporting cells, but is not sharply separated from the unmodified mesenterial epithelium. The mesoglœa is not swollen or bifurcated, and the endoderm immediately behind never becomes lobed. Such incipient filaments occur on the secondary mesenteries of *Orbicella* and *Cladocora* (fig. 57*a*), and a somewhat further stage is represented by *Solenastræa* (fig. 85). The figures should be compared with the early stages in the development of the filament met with in larvæ (Pl. XV), and also in *Porites* (fig. 38). There is the closest resemblance between the two phases, leading to the conclusion that phylogenetically they represent similar structures, whether continuous with the stomodæal ectoderm or remaining free from it.

GLANDULAR MODIFICATIONS.

The filaments of many species of corals undergo a peculiar histological modification, the organs within restricted limits becoming almost wholly glandular. In the fresh tissues, the alteration is indicated by the part being of a golden yellow color, instead of the usual dull white; while in preserved material the same parts are much darker than the rest of the filament, above and below. A transverse section through one of these modified regions, taken from *Orbicella annularis*, is represented on Pl. IX, fig. 69. The filament has become enlarged in diameter, and its cellular constituents are remarkably uniform in character. The latter are long, clearly defined, columnar cells, radiating in a fan-like manner from the expanded mesoglœal base. Each cell is filled with a finely granular substance, and on staining a nucleus is rendered visible. The free margin presents no indication of ciliation, but, in places, globules of some liquid appear in the act of oozing out, while the organ is enveloped in some secretion, evidently issuing as the polyp was preserved. The secretion is of a faint yellowish color, slightly different in refraction from the Canada balsam in which the sections are mounted. The same filament, as it appears in a partly tangential section, is represented in fig. 70. The cells in the middle are cut transversely, while peripherally they are seen more lengthways. The well-defined polygonal outline of each cell in transverse section is very characteristic.

After maceration, the preparations (fig. 71) reveal that the filament comprises only two kinds of cells: (*a*) long, columnar gland cells, of the same diameter throughout, and charged with granular matter; and (*b*) equally long, narrow supporting cells. Nematocysts are altogether wanting. The modification extends over a very restricted vertical range, for on following the sections of the filament, both upward and downward, the normal, more complex structure soon appears.

The actual presence in some cases of a secretion surrounding the filament, and the character of the cells themselves, leads to the conviction that the structure represents a purely glandular organ. Such a histological specialization is very exceptional among Zoantharian tissues. One of the functions of the ordinary mesenterial filament is deemed to be the production of a digestive secretion, and it is manifest that in these special filamental regions an increase in size and number of the secretory cells has taken place, to the exclusion of nematocyst and other cells, with the exception of the ever present supporting cells.

A comparison with the section through the unmodified region of the same filament, represented in fig. 72, at once suggests the manner in which the alteration has taken place. The portion of the mesentery included in the figure is at first very narrow, but just behind the filament its epithelium and mesoglœa become swollen, and as the latter enters the filament it is flattened, terminating in a branch to each side. The boundary between the filament and the swollen mesenterial endoderm is clearly defined. The comparison of fig. 69 and fig. 72 renders it evident that in the former the whole of the filament has taken on the glandular character, while the unmodified basal area is the swollen mesenterial epithelium, now, however, so closely apposed to the filament, as to be distinguished only histologically.

Intermediate stages in the production of the glandular organ from the normal filament are afforded by the filaments of *Mæandrina* (Pl. XXI). A transverse section of one of these is represented in fig. 144; the right side of the filament presents the usual histological details, while to the left side most of the cells have become enlarged and glandular. In lower sections the whole of the filament takes on this latter character, becoming at the same time much larger (fig. 145).

The glandular cells in *Mæandrina* differ from those in *Orbicella* only in the fact that the contents of the cells are a brighter yellow in color; being unaffected by stains, they stand out as very conspicuous areas in microscopic preparations. In *Favia fragum* also the contents are bright yellow.

The glandular modification appears to be somewhat generally distributed, having been found in *Orbicella acropora*, *Mæandrina labyrinthica*, *Favia fragum*, and *Colpophyllia gyrosa*. Its occurrence appears to be somewhat sporadic. Only a few of the filaments in any one polyp undergo the alteration, and its vertical extent is always very limited. In *Orbicella* and *Favia* two or three mesenteries, out of the usual twelve pairs, are thus distinguished, and in *Mæandrina* the proportion is much the same. In one instance, in a portion of the brain coral, the two mesenteries of a pair were thus altered.

A still further development in the same direction is presented by the filaments of *Mæandrina* (fig. 145). In transverse sections of ordinary filaments, the endodermal lobes immediately behind are not sharply marked off from the rest of the mesenterial epithelium; the cells are exceptional in the amount of vacuolization, and the comparative paucity of the zooxanthellæ, but are not essentially different from the ordinary mesenterial endoderm (fig. 143). Where the glandular alteration has taken place, the cells, not only of the filament, but also of the mesenterial epithelium for some distance behind, are nearly all of a uniform character, and the elongated nuclei of the supporting cells are arranged in a zone. In fig. 145, three, coarsely granular, gland cells are represented, the granules staining very deeply, but the remainder of the cells are filled with an extremely fine granular matter, which stains but slightly. The nuclei of the cells are oval, and distributed through the tissue with an approximate uniformity, and perfectly clear gland cells are altogether absent. Instead of the filament being separated from the mesentery by a distinct groove on either side, as is the case elsewhere, its cells are directly continuous with those of the mesenterial epithelium, and these latter have undergone a like glandular modification for some distance, passing gradually into the ordinary mesenterial endoderm.

Thus the elements of two different tissues—filamental and mesenterial endoderm—may assume a like specialized character.

MESENTERIAL FILAMENTS OF MADREPORA AND PORITES.

The histological characters of the mesenterial filaments of *Madrepora* are such as to call for special note. A transverse section of one of these is represented on Pl. II, fig. 14. The mesoglœal lamella from the mesentery enters a short distance into the base of the filament, and there bifurcates; the two halves are directed backward into the lateral regions, where they thin out and are lost. The filament thus becomes divided into three distinct areas, a larger antero-lateral area, and two smaller posterior crescentic regions, each characterized by special histological elements. In front the cells consist of long, narrow, supporting cells, amongst which are numerous clear and granular cells, and a few small thick-walled nemtocysts, though the latter are plentiful only in the proximal region. The cells of the posterior crescentic areas are all of one kind—narrow, ciliated, supporting cells, with the deeply-staining nuclei wholly restricted to the inner two-thirds of the cells (fig. 13*b*); the ciliation is also stronger than anteriorly. Though some such differentiation between the middle and posterior areas of the filaments is found in other coral polyps, the distinction is rarely so marked as in *Madrepora*. In sections stained in borax carmine the posterior regions are an intense red, and present a sharp contrast with the rest of the filament.

The middle region corresponds in histological detail with the glandular streak of the middle lobe of the Actinian filament; while histologically the crescentic areas most distinctly recall the ciliated bands of the lateral lobes of the Actiniæ. In these latter the ciliated bands are constituted wholly of ciliated supporting cells, and the condition in *Madrepora* serves to demonstrate how similar, highly specialized tissues may recur in different regions. The marked development of the lateral ciliated area in *Madrepora* may be conceived as associated with the complex circulatory system of the porose corals, but the weakness of the filaments in the allied genus *Porites* scarcely bears out such a suggestion.

Mature polyps of *Porites* usually contain four pairs of complete mesenteries in the upper region, but the dorsal directives often become free before the lower termination of the stomodæum is reached (figs. 30, 41). Mesenterial filaments, however, are found on only the three remaining pairs of mesenteries, I, II, III; the free edge of pairs IV, V, VI is covered with the ordinary mesenterial epithelium (Pl. III, fig. 29). For a short distance below the stomodæum the tips of the older mesenteries are provided with a deeply-staining tissue, in no ways distinguishable from the stomodæal ectoderm with which it is continuous (Pl. IV, fig. 38); and no sharp boundary line here separates the filament from the rest of the endodermal epithelium. Some distance below the stomodæal region, however, the filament takes on the normal character, and lateral endodermal lobes may be formed on the first and second pairs (fig. 39), though they persist for a very short vertical distance.

The limited development of the mesenterial filaments in *Porites*, on only two or three of the pairs of the mesenteries, is in close agreement with the results of Fowler (1888) upon polyps of *Seriatopora*. In *S. subulata* Fowler found the mesenterial filaments to be well developed on only one pair of mesenteries, the two marked 3 and 10 in the author's notation, and corresponding with the pair marked I, I in the present paper; the mesenteries numbered 1, 5, 8, 12, corresponding with pairs II, III, were generally devoid of any "filamentar" thickening. The proportional development of the filaments thus corresponds with the order of appearance of the mesenteries.

EXTRUSION OF MESENTERIES AND FILAMENTS.

In corals reproducing by gemmation the filaments are rarely so strongly developed as in fissiparous species. In the latter, certain of the filaments are more important than others, and become greatly folded and convoluted, attached to the free edge of the mesentery all the way (Pl. XXII, fig. 148). The mesenteries bearing such strongly developed filaments are capable of partial extrusion through the walls of the polyp, either upon irritation or injury to the latter, sometimes in such quantities as to nearly hide the surface of the colony. Extrusions may appear at any part of the column wall or disk, as well as through the mouth. In the living polyp the mesentery and filament sent out are easily distinguished one from the other; the former is usually thin, colorless, and transparent, while the latter is opaque white, and disposed in irregular loops and coils. The extruded mesenteries in some species are faintly green in color, perhaps due to the large number of zooxanthellæ in the endodermal epithelium. In polyps preserved with the mesenteries thus partly extruded, some of the filaments are also found displaced within the upper polypal regions, and even within the chambers of the edge-zone. In *Cladocora* the filaments have been observed to enter the tentacular cavities, and occasionally they are found in the perithecal continuations of the polypal cavity.

The phenomenon takes place most readily in fissiparous genera, upon strong irritation or after rough handling of the colony, and the extrusions are more copious in these forms than in genera reproducing by gemmation, but probably there are few corals in which it may not occur occur to a greater or less degree. It has, however, never been observed in the numerous colonies of *Siderastræa* kept under observation.

Examination of the column wall and disk of the polyps, under ordinary conditions, fails to reveal any apertures comparable with the "Cinclides" of the Actiniaria, through which it may be supposed that the filaments can pass. The absence of cinclides, and the irregular disposition of the extrusions over any part of the column wall and disk, make it evident that the openings are merely temporary, and capable of formation at any point, structural continuity being again established when the mesenteries are indrawn. On examining the surface of the column wall, immediately on withdrawal of the filaments, the apertures could be observed, and have been found to remain open for a short time; gradually, however, they close over, and all evidence of their former presence is lost.

On Pl. VIII, fig. 64, is given a section through the infolded apical region of *Orbicella*, in which the filament, and the mesentery to which it is attached, are shown in the act of passing through an actual perforation of the column wall. The extra-polypal portion of the filament is charged with numerous, large, thin-walled, oval nematocysts, and the disrupted column wall reveals no histological peculiarities.

The extrusions from coral polyps can scarcely be compared with the ejection of "Acontia," a phenomenon characteristic of the Sagartinæ among the Actiniaria. Acontia are thread-like structures, which are but feebly attached to the mesenteries, and pass through permanent apertures (cinclides) in the column wall of the polyps, or through the mouth, the mesentery in no ways following. If not wholly liberated from the polyp, the acontium can be indrawn. The extruded filaments of corals, on the other hand, still retain their normal position along the contorted edge of the mesentery, and a portion of the latter passes out along with them. The function of both is probably the same, as in each case the organs are strongly charged with nematocysts, and less so with gland cells.

ORIGIN OF MESENTERIAL FILAMENTS.

Probably there is no subject affording greater diversity of opinion among writers on the Anthozoa than that of the ectodermal or endodermal origin of the mesenterial filaments. In the Alcyonaria the problem has been made the subject of special study by E. B. Wilson (1884); in the Actiniaria, by McMurrich (1891); while H. V. Wilson (1888) has made it the object of lengthy notice in the coral *Manicina*.

The actual facts of the case are briefly as follows: In the adult polyps of all three groups, the stomodæal ectoderm is in absolute continuity with the mesenterial filaments of the complete mesenteries, as the latter become free at the lower termination of the stomodæum, and the two agree closely enough in their histological detail to suggest a common origin. Further, the filament differs markedly in structure from the mesenterial endoderm, and would thus appear to have no connection with this layer. Likewise in very early larval stages, the same unbroken passage from the stomodæal ectoderm to the filament is often found to exist, though rudiments of the filaments may be present on the primary mesenteries before or independently of their union with the stomodæum. Were the complete mesenteries only to be taken into account, as in the Alcyonaria, the problem would be much simplified, but in both Madreporaria and Actiniaria exactly similar filaments to those on complete mesenteries are found on the incomplete mesenteries, which remain free from the stomodæum, and hence are never in continuity with its ectodermal lining.

The independence of the filamental and stomodæal tissues within the early larva or bud, along with their histological difference, led E. B. Wilson to regard the six ventral filaments in the Alcyonaria as endodermal; on the other hand, the apparent continuity with the stomodæal ectoderm of the two dorsal filaments from the beginning, and the closer histological resemblance of the two structures, caused Wilson to regard these as ectodermal.

From evidence of a like character, McMurrich, in 1891, came to the conclusion that the Drüsenstreif or glandular streak on the middle lobe of the Actinian filament is of endodermal origin, while the ciliated bands on the lateral lobes are ectodermal. Returning to the controversy in 1899, McMurrich, from his investigations of the mesenterial filaments in *Zoanthus sociatus*, again concludes that the ciliated bands must be conceived as ontogenetically distinct from the glandular streaks. Regarding the ectoderm and endoderm of the Cœlentera as representing but an approximation to the diblastic condition of the higher groups, McMurrich is constrained to regard the distinction between an ectodermal and endodermal origin of any of the organs as of relatively little moment. With this understanding, he concludes: "the ciliated bands are probably in all cases ectodermal, and that in some mesenteries at least, the glandular streaks are endodermal, yet I am prepared to accept as correct the ectodermal origin of the glandular streaks in other mesenteries." The "intermediate" epithelium of the trilobed Actinian filament McMurrich is inclined to regard as ectodermal; my own observations, on species where it is favorably developed for study, lead me to consider it as endodermal.

The structural uniformity of the filaments in all Madreporaria, and the absence of lateral lobes bearing ciliated bands, simplifies the matter somewhat in this group, as compared with the Actiniaria. From its relationships to the mesentery, its form and histological structure, the Madreporarian filament for the greater part of its course undoubtedly corresponds with the middle lobe of the Actinian filament. In the simple condition of the latter, the organs are indistinguishable in the two groups, and without doubt a common phylogenetic origin must be assigned them.

In connection with the origin of the filaments, H. V. Wilson was the first to attach importance to a reflection of the stomodæal ectoderm, which takes place at the inner termination of the stomodæum. This occurs in both adult and larval polyps. On Pl. VI, fig. 51, representing a transverse section through the terminal stomodæal region of an adult polyp of *Cladocora*, the ectoderm is seen to line not only the outer surface of the wall, but has also become folded round the edge of the stomodæum, and comes to occupy the inner or endodermal surface of the organ, thence passing for some distance along both faces of the complete mesenteries, and seeming to give rise to the mesenterial filaments as the mesenteries become free. Similarly, on the left side of fig. 56, a vertical section through the stomodæum of *Cladocora*, the ectoderm becomes folded at the termination of the wall, and is then continuous with the mesenterial filament. The right side of fig. 2 shows the same relationship in *Madrepora*.

On Pl. XIV, fig. 112, a transverse section through an early larva of *Favia*, also displays a tissue on the endodermal surface of the stomodæum, in all respects resembling that of the stomodæal ectoderm. Separated by the first pair of mesenteries, it forms a distinct, deeply-staining lobe, in both the larger and smaller primary chambers, and differs greatly from the surrounding endoderm. In sections a little higher, the reflected ectoderm is wholly wanting, and the stomodæal lining is purely endodermal (*cf.* figs. 126, 127).

The stomodæal ectoderm, reflected in this way around the lower edge of the stomodæal wall, occurs to a greater or less degree in probably all Madreporaria. Invariably, the mesenterial filaments of the complete mesenteries seem as if they took their origin from it, and the histological resemblance is very close. The extent of the reflection along the cœlomic surface of the stomodæum, and also outwardly along the mesenterial faces, varies much with the amount of retraction or expansion of the polyps, for in the latter condition the stomodæal wall and edge of the mesentery come to be almost in the same vertical straight line, and no reflection is then apparent.

Wilson, in his studies of the early larvæ of *Manicina*, found the stomodæum to be applied to the column wall, and its ectoderm appeared to pass down the inner surface of the wall, even before the first pair of mesenteries had appeared. In later stages the ectoderm of the stomodæum was reflected up the endodermal surface, and all the primary mesenteries, except the first pair, were considered to receive their filamental tissues from these ectodermal tracts, though some filaments were found to be present on the mesenteries before the union of the latter with the stomodæum had been effected. With regard to the origin of the filaments on the mesenteries which never reach the stomodæum, probably few students of the embryology of the Anthozoa will be prepared to follow Wilson in his suggestion (p. 220) that these receive their ectoderm from a reflection along the entire length of the cœlomic surface of the stomodæum and peristome (the epithelium *x*. of Wilson's figs. 50 and 55). Its acceptance, in the case of the incomplete mesenteries of some species, would demand that the inner lining of nearly the whole of the upper region of the polyps should consist of ectodermal tracts.

A typical example of the condition of the filaments found in larvæ is presented by the transverse sections of the larva of *Favia fragum* represented on Pl. XIV. For the greater part of its length the inner (cœlenteric) layer of the stomodæum resembles the rest of the endoderm, but toward the internal end it begins to assume a histological character more nearly resembling that of the ectodermal lining. The cells are now narrow and closely arranged, and the numerous brightly-staining nuclei form a definite zone, marking off the region very distinctly from the ordinary endoderm. This is the so-called "reflected ectoderm" of Anthozoan literature. In *Favia* it passes along the first pairs of mesenteries for a short distance, and as these sever their connection with the stomodæum they are tipped with a tissue of like nature. Increasing in extent, it is continued as the mesenterial filament along the edge of the first pair of mesenteries, almost as far as their termination at the aboral end of the larvæ, ceasing on one mesentery a little in advance of the other (*cf.* also Pls. XVIII, XXV).

At this early stage the mesenterial filament is not sharply marked off, except histologically, from the rest of the mesenterial epithelium. Its numerous nuclei stain brilliantly in borax carmine, and structurally it is indistinguishable from the stomodæal ectoderm. This resemblance, combined with the absolute continuity of the two at the commencement of the filaments, would seem to remove all doubt that the two—stomodæal ectoderm and the mesenterial filaments—are of one and the same origin.

But the conclusion becomes less certain when the incomplete mesenteries are taken into account, for along their free edge is a tissue of exactly similar nature; yet the mesenteries are in no way connected with the stomodæum, and there is no apparent means by which the incipient filament can have been in unity with its ectoderm.

The early appearance of the filaments on the second pair of mesenteries is represented in fig. 112, from a section taken a little above the termination of the stomodæum. At first only one mesentery displayed any marginal modification, but in the figure the filament has appeared on the other member of the pair, while below it is as strongly developed on both as on the first pair of mesenteries, but disappears in advance of the filament of the latter. In some of the sections coming below that represented in fig. 112 there is the feeblest hint of the filament on the mesenteries of the third pair, which scarcely extend beyond the endodermal lining.

It is manifest therefore that the filaments on the second pair of mesenteries originate quite independently of any connection with the stomodæum and of the reflected ectoderm. From a study of the conditions in both the third and the second pairs it is inconceivable how at any earlier stage, say before the middle embryonic tissues had broken down, that any such connection could have been established. The reflected ectoderm passes backwardly but a short distance along the cœlomic surface of the stomodæum, and there is no possibility of its working its way upward, across what represents the disk, and then downward along the free edge of the mesentery. The presence of filaments on the second pair of mesenteries before union with the stomodæum would imply that a similar development may also take place on the third pair of mesenteries before their union, and sections reveal that such actually occurs. It is also manifest from the sections, that before the union of the mesenteries with the stomodæum is effected, there is no means by which the free margin of the former can have come into contact with the reflected ectoderm.

From the conditions represented in the larvæ of corals generally, the conclusion is reached that the mesenterial filaments may originate independently of any connection with the stomodæal ectoderm, and may therefore be assumed to be endodermal.

The filaments on both the complete and incomplete mesenteries at the early stages of larval development present but little histological differentiation, except in the case of the filament on the first mesenterial pair. They consist mainly of supporting cells, and stain much more deeply than the ordinary endodermal lining, but gland cells and nematocysts are scarcely determinable. Similar details are often presented by the edge of adult mesenteries, which always remain free from the stomodæum, showing that in the orders beyond the primary the filaments originate in the same manner. In these cases the filaments may never become fully developed, but remain in an incipient or rudimentary condition. This is illustrated by the mesenteries of *Orbicella acropora*. The six pairs of mesenteries of the first cycle are complete, and filaments are well developed below; similar filaments appear on the mesenteries of the second cycle, which fail to reach the stomodæum; but on the third cycle of twelve pairs the mesenteries are merely tipped with a deeply-staining tissue, which is indistinguishable from that on the filaments of larvæ. Further, some mesenteries bear incipient filaments only in their upper course, while the organs are fully developed below. *Cladocora arbuscula* also affords similar illustrative examples (Pl. VII). The edge of a mesentery in its upper course is represented in fig. 57 *a*, and the filament is seen to be quite rudimentary; below the stomodæal region, however, the filament on the same mesentery is fully formed (fig. 57 *c*). If the filaments of the incomplete mesenteries originate from a reflected tract of stomodæal ectoderm, it might reasonably be expected that they would be best developed in the uppermost region of the polyp, whereas, as a matter of fact, they are here absent or only incipient, even when fully developed below.

All the evidence seems to favor the view that in the Madreporaria the mesenterial filaments first appear independently of any connection with the ectodermal lining of the stomodæum, but that in the case of the complete mesenteries such a continuity is early established, while with incomplete mesenteries the separation is permanent.

When describing the adult mesenteries, it is shown that the first part of the filament differs in form and structure from that below, and histologically is indistinguishable from the stomodæal ectoderm, with which it is in direct continuity. It is manifest, therefore, that between the actual stomodæal termination and the commencement of the true filament there is a tract which partakes more of the nature of the stomodæal ectoderm than of the filamental tissue. It forms the connecting link, as it were, between two tissues which may be considered as wholly distinct both phylogenetically and ontogenetically. Such, it may be conceived, is the significance of the "reflected ectoderm" as seen in corals. It is the stomodæal ectoderm passing along the mesentery to establish structural continuity with the upwardly growing filament.

The strongly ciliated character of the stomodæal ectoderm marks out the layer as specially concerned in the circulation phenomena of the polyp, and the same must be affirmed to a less degree of the upper part of the mesenterial filament. For the proper carrying out of this it is manifest that a close histological continuity should be maintained between the two structures, and it can be conceived that in establishing this the stomodæal ectoderm passes some distance down or along the mesenterial edge to meet the upgrowing filament proper.

The mesenterial filaments on the incomplete mesenteries are the homologue of those on the complete filament, but the latter are in more or less direct histological continuity with the stomodæal ectoderm by a downgrowth from the latter, while the others are free throughout.

In his recent paper (1900, p. 73), Appellöf contends for the ectodermal origin of the whole Actinian filament, his fig. 25 showing a distinct passage of the stomodæal ectoderm down the free edge of the mesentery. The occurrence of an interval of endoderm between the stomodæal ectoderm and early filament, such as McMurrich (1891) and I (1899) have found in other larvæ, Appellöf would explain as the result of a more or less accidental severance of continuity upon retraction of the larvæ. Such a suggestion would scarcely be applicable to the conditions already described in the larvæ of *Favia*, for the first indications of the filamental tissue occur at very different levels on the various mesenteries, in some instances at a considerable distance below the stomodæal termination. On the view presented above, the appearances which Appellöf describes in *Urticina* are not directly concerned with the formation of the filament; the downward growth of the ectoderm from the stomodæal wall is merely the means of establishing continuity with the true filament which will appear independently below.

BASAL DISK, SKELETOTROPHIC OR SKELETOGENIC TISSUES.

Under these terms will be included the three Cœlenterate layers ectoderm, mesoglœa, and endoderm—which everywhere cover the surface of the skeleton in the living portion of a coral. G. von Koch (1882) has fully demonstrated that the ectoderm alone is the true skeletogenic layer, and is actually adherent to the corallum; but it is convenient to study along with it the associated mesoglœa and endoderm. The early stages in the growth of the young polyp after fixation (Pl. XIX) reveal that the basal disk only is concerned in the formation of the skeleton, and therefore all the subsequent foldings, invaginations, and evaginations of the skeletotrophic tissues are but so many extensions of this region of the polyp, produced *pari passu* with the deposition of the calcareous particles. The theca, septa, costæ, columella, and all the teeth, spines, etc., connected with them, represent so many foldings of the basal disk, for all take their origin from the same continuous layer, and their surface remains covered by it so long as they belong to the living parts of the polyp.

In most instances, and especially in the perforate corals, the skeletotrophic layers comprise the greater proportion of the soft parts of the colony upon decalcification. The superficial tissues as a whole—column wall, tentacles, and disk—are always much less in superficial area than the skeleton-covering tissues. The polyps, as a rule, extend a little more deeply within the skeleton than is the amount of their expansion above.

To study with any degree of success the skeletotrophic tissues of a coral, it is necessary that decalcification be carried out. Lining the corallum so very closely, it is impossible to make a minute examination of the polypal layers *in situ* with the thinness to which sections of the skeleton can be ground. In the process of dissolving away the skeleton by means of acids, scarcely any distortion of the tissues appears to take place if the latter have been properly hardened, and the same may be said of the histology of the skeletogenic layer.

The polypal region set free by decalcification is very complicated in its detailed characters, and varies greatly for each genus. An exact representation may be obtained by making a plaster cast of the surface of any dried coral, and then dissolving away the latter. The superficial tissues seen in the living or preserved colony are found to represent but a small proportion of the polyp. The space formerly occupied by the thecal wall is now free, and in the case of gemmiferous species each polyp presents much more individuality than under ordinary conditions, while in fissiparous genera, like *Mæandrina* and *Colpophyllia*, the polypal systems stand out as very distinct, continuous ridges, separated laterally by deep grooves formerly occupied by the collines. The septal and columellar projections are now represented by so many deep lateral and vertical inturnings of the polypal tissues, and their arrangement can be studied in detail, though adding little to what is obtainable from the skeleton itself.

The height of the decalcified polyp gives the depth to which in the living condition the soft tissues extend downward within the corallum, revealing how comparatively superficial in every case is the living portion of a colony. For example, after decalcification the polypal tissues in *Porites astræoides* vary from 3 to 5 mm. in thickness; the polyps of *Siderastræa radians* are 3 mm. in height when freed from the skeleton, and those of the larger *S. siderea* are 6 mm. Polyps of *Orbicella acropora* scarcely extend for 1 cm. within the skeleton of the colony, and the same is the case even with the polypal systems of the large colonies of *Mæandrina*.

In the upper region of decalcified polyps the skeletotrophic walls as a rule present a different structural appearance from those below. Above, they are more transparent and delicate looking, but as the lower region is approached the walls gradually become firmer in character, white, and strongly opaque. This structural alteration is seen in nearly all the forms examined, and is evidently due to the pronounced histological change, referred to below, which takes place in the endoderm in passing from above downward.

Histologically the three skeletotrophic layers differ much among themselves, and also in different regions of the polyp. They will now be described as seen in sections.

ENDODERM.

In the upper part of any polyp the skeletal endoderm, as a rule, closely resembles that of the column wall, disk, and mesenterial epithelium; or, as in Pl. XVIII, fig. 129, it may be somewhat narrower, being represented by a very simple columnar epithelium. Gland cells of various kinds, supporting cells, and scattered zooxanthellæ are the usual constituents, but no trace of any muscular fibrils nor of a nerve layer has been found.

As the more proximal regions of the polyps are approached, the layer begins to undergo a peculiar modification. It becomes much broader and is highly vacuolated, exhibiting in sections a delicately reticular structure, the individuality of the cells being wholly lost (figs. 129, 73), while the chief constituents—nuclei, cytoplasm, zooxanthellæ, and the contents of the few granular gland cells—are mostly accumulated in a marginal zone. The differences in character between the endoderm in the upper regions and below are represented by figs. 44, 45, and 73, 75. In *Orbicella* (Pl. X, fig. 73) the layer is 0.1 mm. broad below, while above it is about 0.03 mm. in thickness (Pl. IX, fig. 68).

In some species the thickened endoderm is crowded throughout its extent with granules of various size, which render the layer dense and nearly opaque in sections. This is especially characteristic of *Astrangia solitaria* (Pl. V, figs. 44, 45) and *Dichocœnia stokesi*. The granular particles are usually non-staining, and are thus distinguished from the nuclei which are also present, situated near the margin. In *Dichocœnia* the granules are green (p. 439). Very rarely they are arranged as if constituents of an oval cell; more usually they are scattered uniformly through the whole or part of the layer, without any suggestion of being contained in special gland cells. The condition in the lower skeletal endoderm of *Solenastræa*, represented on Pl. X, fig. 79, is somewhat intermediate; large cells full of coarse granules occur, and in addition to these are many isolated granules.

The thickened skeletotrophic endoderm of the fissiparous genera *Mæandrina*, *Manicina*, *Colpophyllia*, and also *Orbicella* has very few contents; a few small scattered nuclei, here and there a zooxanthella, and perhaps a few granules, are all that can be made out, the layer being vacuolated in either a rounded or irregular manner. In the porose genera *Madrepora* and *Porites* practically no modification occurs; the skeletotrophic endoderm is much alike in character in all parts of the polypal cavity, as well as in the canalicular outgrowths. Also in *Siderastræa* scarcely any difference is apparent between the upper and lower skeletotrophic endoderm (Pl. XXIII, fig. 156). This genus is further exceptional in that the calicoblast ectoderm remains a broad layer throughout.

The great thickening of the endoderm sensibly diminishes the mesenterial loculi below; while the comparative fewness of the nuclei, their small size, and the sparse protoplasmic contents would indicate that the cellular activity is much diminished compared with the upper regions of the polyp.

Wherever the calicoblast layer is in an active condition the endoderm overlying it presents a corresponding state. In the upper parts of polyps, where skeletal growth is proceeding as a result of the activity of the calicoblasts, the endodermal cells overlying the latter are highly protoplasmic, stain deeply, and present all the evidence of functionally active cells. A marked instance of this occurs in connection with the aboral termination of the interseptal loculi. It is here that from time to time the dissepiments are formed which cut off the polyp from the lower portion of the corallum; below the last dissepiment the skeleton may be considered as dead, while above it is covered with the soft polypal tissues. The production of dissepiments must be constantly taking place in a vigorously growing coral, hence the calicoblasts at the actual base remain in a more or less permanent condition of activity, as represented on Pl. X, fig. 73. The figure shows that the columnar character of the cells is limited to the actual flat base of the chambers, the calicoblasts being insignificant along the lateral walls. Fig. 73 is also specially instructive as showing how the endoderm immediately overlying the active calicoblast layer differs from the layer on the lateral walls, where the calicoblasts are non-active. The endoderm has become much thinner, the cells are fully charged with protoplasmic contents, and stain deeply.

The skeletotrophic endoderm overlying the upper parts of septa which may be supposed to be in a growing condition, is also much thinner than that lining the wall of the calice and inner parts of the septa at the same level. This diversity is very marked in fig. 129, Pl. XXIII, representing a mesentery of *Mæandrina* with the skeletotrophic tissues associated with it.

It is manifest that the outer calicoblasts can obtain their nutriment and the calcareous salts wherewith to form the dissepiments only in so far as these pass through the overlying endoderm and mesoglœa; hence wherever the former are in a functionally active condition the endoderm would be expected to show a corresponding modification, as compared with regions where it overlies non-functional cells.

MESOGLŒA.

The mesolgœa of the skeletotrophic tissues is nearly everywhere a thin lamella, but, as a rule, it thickens a little along the line of attachment of the mesenteries to the corallum. At this place, and more or less scattered over the whole surface, are found peculiar cone or wedge-shaped structures which appear as processes of the mesoglœa. In sections the processes are striated toward their free extremity, which in methyl blue and in carmine always stains much more deeply than the remaining mesoglœa. Their function would seem to be to bind the soft tissues to the corallum. Where the insertion of a mesentery on the column wall is seen in longitudinal section the processes appear as represented in fig. 95, Pl. XIII.

The nature and origin of the mesoglœal processes has been specially studied by Bourne (1899). He shows that they are formed from special ectodermal cells which he terms *desmocytes*. These take their origin from certain cells in the calicoblast layer, and become secondarily attached to the mesoglœa. The processes thus formed may be known as desmoidal processes, though Bourne employs the term desmocyte for them, as well as for the cells by which they are produced.

The desmoidal processes may occur at any part of the outer skeletotrophic tissues, but are most numerous in areas along which the tissues may have to withstand, as it were, the strain of any muscular activity of the polyp. The attachment of the mesenteries to the skeletotrophic tissues represents such areas, and here desmoidal processes usually occur in numbers.

Also, as shown in fig. 67, Pl. IX, they are specially developed in colonies along the line of separation of one polyp from those adjacent. It is obvious that at the point *des. pr.* the polyp upon expansion will tend to raise the skeletal covering from its adherence to the edge of the calice; hence to meet this the skeletotrophic tissues are provided with a special development of desmoidal processes. However fully expanded a polyp may be, it is never able to detach its basal wall from its adherence to the corallum.

The whole manner of distribution of the desmoidal processes fully supports Fowler's (1899) suggestion that the structures are special devices for maintaining the adherence of the polypal tissues to the skeleton. Their purpose in many ways is comparable with that of the ligaments in the higher animals. They do not occur over the actively growing regions of polyps: the skeletotrophic ectoderm is here a continuous epithelium (Pl. II, fig. 8).

ECTODERM OR CALICOBLAST LAYER.

The basal ectoderm or calicoblast layer is of much importance in studies of the morphology of the Madreporaria, seeing that by it is produced the entire skeleton, or coral as popularly understood. The nature of the layer, and the mode of formation of the skeleton by it, have been the subject of much controversy, with which the names of Milne Edwards and Haime, A. R. von Heider, G. von Koch, Miss Ogilvie, and G. C. Bourne are associated. Bourne (1899) has recently summarized the various views as to the structure and formation of the skeleton, and has made a very thorough study of the process as it takes place in different genera of Anthozoa. With regard to the Madreporarian skeleton he finds, with von Koch, that the calicoblast layer is everywhere a simple epithelium, the cells rounded, columnar, or fused together, and that the calcareous matter is laid down wholly external to the polyp. He thus differs from von Heider and Ogilvie, who concluded that the calicoblast ectoderm was a multilaminar layer, and that the skeleton resulted from calcification within the cells. The calicoblasts described by von Heider are shown to correspond with the desmocytes of Bourne, and are not concerned with the secretion of the skeleton.

The results from the present study fully confirm those of von Koch and Fowler as to the unilaminar condition of the calicoblast layer and the ectoplastic formation of the skeleton. Usually the layer is only well developed within regions of active growth, as toward the uppermost part of the corallites (Pl. II, fig. 8), or aborally, where dissepiments are in course of formation (Pl. X, fig. 73). Elsewhere the calicoblasts form an extremely flattened layer; in *Siderastræa*, however, the structure is the same practically throughout the whole of the skeletal area (Pl. XXIV). As a rule desmocytes are wanting where the calicoblasts are well developed, but are plentiful where the cells are nonactive, especially along the line of attachment of the mesenteries to the basal wall.

In some instances (*Madrepora*, fig. 16) the skeletogenic ectoderm shows distinct cell limitations, as in ordinary columnar epithelium; but generally these are lost, and the contents are arranged in a continuous manner and largely vacuolated.

Between the calicoblast layer and the actual skeleton, Bourne has found what he terms a *limiting membrane*, separating the polypal wall from the calcareous matter. This occurs wherever decalcification of properly preserved material is carefully carried out, but to my mind represents the remains of the colloidal matrix in which the skeleton is deposited. At the growing apex of *Madrepora* a continuous ground substance remains after decalcification, and fills the whole of the space occupied by the corallum, behaving toward reagents exactly like the mesoglœa between the ectoderm and endoderm. It presents a striated, scale-like appearance, altogether similar to that of the calcareous fibers of the skeleton of *Madrepora* (figs. 18, 19). The striæ have manifestly been produced by the calcareous skeleton laid down within a perfectly homogeneous substance. This latter is evidently secreted by the calicoblasts, but only under the most favorable conditions, as near the actual tip of rapidly growing branches, can it be found persisting throughout the skeleton. Elsewhere the organic matrix has either wholly disappeared, or is so insignificant as not to persist in a continuous form on decalcification. Stages in its disappearance can be easily followed in *Madrepora*, in passing downward from the apex of branches, and it becomes obvious that the mesoglœa-like covering on the outside of the calicoblast layer is but the densest, most recent part of the matrix, which is persistent, and within which calcareous fibers will be deposited.

The skeletotrophic tissues of *Siderastræa* and *Madrepora* will be described in somewhat more detail.

The skeletotrophic layers of *Siderastræa* present certain features which distinguish them from most corals (Pl. XXIV, figs. 157, 160). The endoderm broadens but little in passing from above downward; it is strongly vacuolated throughout, and contains numerous granules and a few zooxanthellæ, but all traces of cellular divisions are lost. The skeletotrophic mesoglœa is everywhere thin, forming only a mere dividing line between the ectoderm and endoderm. The skeletogenic ectoderm has practically disappeared where the mesenterial mesoglœa unites with the body wall, and the mesoglœa has become swollen in a triangular manner, and is finely striate, giving rise to desmoidal processes. The latter are found only in association with the mesenteries, where these unite with the calicinal wall, or more frequently where perforated by synapticula (fig. 159).

The calicoblast layer of *Siderastræa* is remarkable in that it persists as a broad, uniform layer throughout the polyp, even in regions where the corallum may be assumed to be in a less active condition, as along the lateral surface of the septa. Its usual appearance is represented in figs. 157, 160. It is strongly vacuolated, with numerous fine granules which stain deeply, and seem as if constituting a matrix in which the vacuoles are formed. The ectoderm nowhere presents the characteristics of a columnar epithelium; cell limitations are indistinguishable, and larger, deeply-staining bodies among the granules are probably nuclei. Where decalcification has been carefully carried out, fragments of the homogeneous organic ground substance, within which the skeleton is deposited, remain behind, closely adherent to the calicoblast layer.

Sections of decalcified material of *Madrepora* through the growing region at the apex of branches, usually show a broad, columnar calicoblast epithelium, much broader than the ciliated endoderm of the canal system (Pl. II, figs. 8, 16). Cell limitations are more or less clearly indicated, and the cells are largely vacuolated, the protoplasm being finely granular, and more concentrated toward the periphery of the layer. The nuclei are rounded and arranged mostly along a middle zone, but are not as regular in position, nor as numerous, as in the columnar cells of the endoderm. There is no indication whatever that the layer is more than one cell thick, or that transverse cell division ever takes place.

In the first few sections through the actual apex, where the spaces left by decalcification are very narrow, the calicoblast layer is even a little broader than in the sections represented, and the vacuolization is not so pronounced. In sections some distance from the apex, the layer begins to narrow, and soon it is represented by flattened cells which are often scarcely perceptible. This is the condition for the most part throughout the colony, and is inconsistent with much functional activity.

In the most actively growing regions of the colony, where the calicoblast layer forms a broad columnar epithelium, the mesoglœa appears as a uniformly thin layer, entirely free from any connection with the corallum (figs. 8, 16); but in other areas, when decalcification has been carried out slowly, the middle layer displays numerous desmoidal processes on its skeletal surface (figs. 7, 17). The most perfect forms of desmoidal processes are conical or pyramidal, the base projecting outward; usually they are seen in longitudinal section, but occasionally in transverse section. Toward their free edge the processes stain much more deeply than elsewhere, and are very finely striate, the striæ being practically parallel and of equal length. The actual edge of the desmoidal processes is usually jagged, as if torn from some attachment.

Elsewhere the mesoglœal lamella exhibits smaller, less regular elevations, which are similarly deeply stained and striate. When a process is cut through transversely, either radiating striæ are presented at all the levels, or a punctate appearance is revealed. Nuclei are scattered about the origin of the processes, but are never found within it. The processes are undoubted outgrowths of the thin mesoglœal lamella, the actual continuation being readily observed; but the deeply-staining character toward the free edge indicates that some structural alteration has taken place.

Madrepora offers special advantages for a study of the nature and relations of the skeletal matrix, as, owing to the rapid growth taking place at the apex of the branches, the admixture of ground substance and calcareous deposit is here better preserved than in many corals. In apical polyps, which have been hardened in chromic acid, and slowly decalcified by means of weak acetic acid, the organic matrix of the skeleton is obtained *in situ*. It presents exactly the appearance of a striated mesoglœal substance, and behaves toward reagents in the same way, and is wholly devoid of nuclei. The fine striæ are arranged in a scale-like manner (fig. 18). The matrix is best developed at the terminal region of the corallites, and is densest toward the polypal surface, gradually thinning toward what would be the primary center of calcification within the branch. In most preparations it is shrunk from the calicoblast layer.

Looking at fragments of the corallum under a low magnification (about 60) the surface has the appearance of minute imbricating scales. They are somewhat polygonal in outline, and the free edge is directed obliquely forward, the whole indicating a spiral arrangement, most pronounced in the smaller branches. Under a higher magnification, however, each of the apparent scales is seen to be but the exposed terminal portion of an obliquely arranged fiber, proceeding from the deeper regions of the corallum, and the superficial scale-like appearance is produced by the overlapping of the numerous fibers. This is also seen in sections of the skeleton starting from the surface, but the distinction between one fiber and another practically disappears a little below the surface. The free edge of each fiber is often slightly jagged, not rounded and smooth, as if torn from some other connection. Viewed by transmitted light, each fiber has an indistinct, delicate, fibrillar appearance, with alternating lighter and darker transverse bands, somewhat recalling a striped muscle fiber (fig. 19).[a] The matrix left upon decalcification is thus closely repeated in the microscopic characteristics of the newly formed skeleton.

In studying the relations of the corallum to the soft tissues, sections have been made through the apical region of branches in which decalcification has but partly proceeded. It is found that the middle portion or center of calcification is the first to disappear by the action of the acid, the periphery, where most organic ground substance occurs, being last.

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[a] Dr. Ogilvie (1896, p. 217) also gives a figure of the enlarged calcareous fibers of *Madrepora*, terminating in what she considers to be calicoblast scales. According to the view there presented, the scales are calcified calicoblasts, but as shown above the polypal tissues afford no support for such a conclusion. The organic matrix referred to by Miss Ogilvie is proved to be a homogeneous, jelly-like substance secreted by the calicoblast layer, within which the calcareous fibrillæ are laid down in a scale-like manner.

GASTRO-CŒLOMIC CAVITY.

The term gastro-cœlomic is applied to the whole of the internal, endoderm-lined cavity of coral polyps, including any outgrowths or continuations which it may possess. In some ways the designation is preferable to the terms gastro-vascular cavity or cœlenteron, generally employed for the polypal cavity in Anthozoa. For from the considerations of van Beneden (1891), and E. B. Wilson (1884), there seems some evidence to support the view that the space but incompletely inclosed by the mesenterial filaments is the morphological equivalent of the gastric cavity, or enteron, of the higher Metazoa, while the remainder of the internal cavity, partitioned by the mesenteries, is the morphological representative of the cœlom of the Enterocœla.

Among colonial corals the gastro-cœlomic cavities of all the polyps in actual union with one another are in communication, and the nutrient fluid can pass from one to the other. This is a persistence of the conditions consequent upon asexual development, whether this takes place by gemmation or by fissiparity. In gemmation new polyps arise wholly or in part from the column wall of other polyps, and the internal cavities of the two are common for a time. Thus the developing bud of *Madrepora*, shown in the series of figures on Pl. III, arises altogether from the cœnosarcal wall of the colony, and its cœlomic cavity during the primary stages is represented by one of the superficial canals of the colony. In the developing polyp of *Solenastræa*, represented in section in Pl. XII, fig. 87, a distinct partition wall, lined with endoderm on both sides, now partly separates the bud from the parent; but interruptions occur at more or less regular intervals, which permit of a circulation between the two cavities.

The mode of communication of the various polypal cavities in a colony varies somewhat in different forms. In genera like *Porites*, *Siderastræa*, and *Agaricia*, in which the polyps are separated from one another merely along a common calicinal wall, intermesenterial apertures remain along the line of union, while the polyps are partitioned mesenterially. In *Siderastræa* septal partitions also occur, at any rate during retraction; for peripherally the column wall comes to rest directly upon the septal covering, so that only a very narrow space is left on each side between the mesenterial and the septal wall (Pl. XXIII, fig. 156). The channels of communication of four adjacent polyps of *Porites* over the thecal edge are represented on Pl. III, fig. 31, taken from a section through the superficial region of a colony in which the polyps were in a retracted condition. The fragments of the corallum seen are the slightly exsert septa, and the canals pass over and around them.

Adjacent polyps of *Orbicella* and *Solenastræa* are also placed in communication intermesenterially at the superficial line of union of the polyps. During retraction the apertures are not connected directly with the main cavity, but through the intermediation of its perithecal prolongations. The same method of superficial intermesenterial communication holds for the contiguous rows in the genera reproducing by incomplete discal fission, e. g., *Mæandrina* (Pl. XX, fig. 138), *Colpophyllia*, *Manicina*, *Isophyllia*. In these, however, the polyps which are united in the same discal system have no independent cavity, the one continuous chamber is shared in common. The polyps do not attain true individuality; they can best be understood as so many mesenterial and stomodæal systems within a general cavity.

The numerous polyps constituting a colony of *Madrepora* are likewise in communication by means of the superficial canals, which are continuous over the thecal edge with the main gastric cavity (Pl. I, fig. 2); but in the great group to which *Madrepora* and also *Porites* belong—the Porosa—there is another and more complicated system of communication than that afforded by the superficial canals. Anastomosing radial canals are given off by the basal (skeletotrophic) part of the body wall, in such a way that they appear as if penetrating the corallum which separates one polyp from another, and thus place the different cœlentera in union; in *Madrepora* they further come into communication with the superficial canals.

The radial canals are given off very closely in both *Porites* and *Madrepora*, and are disposed both mesenterially and intermesenterially, without any apparent regularity. As many as five or six may be seen in a single transverse section (Pl. I, figs. 3–6). They are not so numerous in the upper region of the apical polyps of *Madrepora* as below. In fig. 2, representing an apical polyp, no radial openings occur on either side, though an uninterrupted continuity of the corallum for such a distance appears to be somewhat unusual. The superficial canals in exsert corallites of *Madrepora* are mostly longitudinal in direction; but transverse connections occur, and the canals may be also interrupted by skeletal growths. Decalcified preparations show that the canal system does not as a rule prolong the gastro-cœlomic cavity at the aboral end of the polyps; in both *Porites* and *Madrepora* the polyps and their canals are abruptly truncated.

The internal canal system in the Porosa is morphologically basal in origin. For it is established that the whole of the skeletotrophic tissue is derived from the primary basal disk, and all its evaginations and invaginations are but so many foldings and complications of the walls of this region of the polyp. The canals of the perforate corals may therefore be compared with the basal communicating canals of colonial Actiniaria, such as those of *Palythoa* among the Zoantheæ. Though exerting a profound influence on the character of the corallum, the canal system of the Porosa has but little morphological significance, and in any natural classification of corals appears altogether unworthy of the importance which has been assigned it by systematists.

The fundamental difference between colonial non-perforate and perforate corals may be thus stated: In the Aporosa the gastro-cœlomic cavities of the component polyps of a colony are in communication only by superficial apertures along the common line of union of the column wall and base, while the Porosa have in addition a means of communication by basal anastomosing canals.

Compared with that of the Actinian polyp the gastro-cœlomic cavity of the Madreporarian polyp is much more subdivided and intruded upon, both radially and peripherally, particularly in its lower region. In addition to the mesenterial partitions, shared in common with the Actiniaria, a like number of radiating septal invaginations usually occurs, while columellar, spinous, and synapticular productions still further break it up centrally and peripherally. Moreover, the calicinal wall itself is often produced upward as a peripheral, circular wall, and, so far as it extends beyond the line of union of the column wall and base, divides the cœlomic cavity, as well as its mesenterial partitions, into inner and outer moieties, the latter constituting the cavity of the edge-zone or Randplatte.

During expansion the upper part of living polyps is elevated for some distance wholly beyond the corallum, and in distinct polyps the free portion is cylindrical, in form closely recalling an Actinian polyp (figs. 46, 48). Here the subdivisions of the gastro-cœlomic cavity are only mesenteric, and are arranged peripherally into entocœlic and exocœlic chambers in a strictly Actinian fashion. The fleshy parts of fissiparous genera likewise become extended for several millimeters, the oral disk appearing as a meandering platform fringed by the zone of tentacles, and the column wall on either side as a nearly vertical sinuous parapet; the cavity is divided into entocœlic and exocœlic chambers, but not with any cyclic regularity.

In retracted polyps not only is the oral region withdrawn within the calice, but the perithecal wall becomes more nearly apposed to that immediately covering the skeleton, and closely reproduces the outer corallar form, thus largely obliterating the intervening gastric space.

Proximally the polypal cavity extends some distance within the corallum, or rather the corallum has intruded within the polyp; and in these lower regions the cavity becomes subdivided in a most complex manner by skeletal ingrowths. In addition, the skeletotrophic endoderm becomes greatly thickened proximally, and further encroaches upon the chambers, but apparently the mesenteries always cease before the lower termination of the polypal cavity is reached.[a]

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[a] Nothing like the peculiar obliteration of the polypal cavity which Sclater (1886) describes in *Stephanotrochus* has been encountered. In all cases the cœlomic cavity persists as far as the proximal floor of the polyp. According to Bourne (1893, p. 219), the polyp in *Fungia* does not desert the lower part of the calice, but remains adherent to the basal plate. Yet even here Bourne finds that the primary and secondary mesenteries are carried upward as growth proceeds, and are confined always to the upper moiety of the calice; the lower moiety consists only of chambers lined with endoderm and undivided by mesenteries.

In the upper region of the calice the septal invaginations as a rule stretch but a short distance radially into the gastro-cœlomic cavity, the portion of the polypal cavity included between one septum and another being spoken of as an interseptal chamber or loculus. As the lower regions are approached, the septa extend farther and farther centrally, subdividing the cavity more and more, until ultimately they unite in the middle to form or share in the columella. Where such central fusion takes place, the gastro-cœlomic cavity is divided into interseptal chambers, which in transverse section are wholly distinct from one another, laterally and centrally (figs. 55, 84). If the septa of all the cycles, both entocœlic and exocœlic, extend as far as the center of the polyp, each chamber is simple, and includes within it only one mesentery (*Solenastræa*, fig. 84); but when younger cycles extend only part way toward the center, each chamber is incompletely subdivided, and may contain two or more mesenteries (figs. 54, 55). All stages toward the complete isolation of the septal chambers are represented in passing a series of transverse sections in review, from above downward, the primary septa being the first to unite centrally. Where the septa do not completely fuse centrally, in other words, where they do not form a solid columella, the interseptal polypal chambers remain in open communication at the middle throughout the polyp (*Mæandrina*, Pl. XXI, fig. 142).

The actual manner in which the interseptal chambers terminate proximally is best studied in entire, decalcified polyps. In some species they narrow gradually in an oblique manner, while in others they terminate abruptly. Where the chambers are oblique, the polyps gradually diminish in transverse area as the lower region is approached, the newer chambers ceasing in advance of the older. This is characteristic of the genera *Oculina*, *Favia*, *Agaricia*, *Mæandrina*, *Manicina*, and *Isophyllia*. In *Orbicella*, *Solenastræa*, *Siderastræa*, *Cladocora*, *Astrangia*, *Porites*, and most *Madrepora*, the polypal chambers are of practically the same sectional area from beginning to end, though the truncation of the newer chambers may occur a little in advance of that of the older. In mature polyps of the last series of genera, the basal floors of the mesenterial chambers may all occur at practically the same level, as if all had been cut off by dissepiments formed simultaneously.

Pl. V, fig. 42, representing transverse sections through *Porites*, shows how the central cavity is encroached upon by the spine-like, columellar projections; according to the level at which the section is made, they may be either distinct or in continuity with the septa. The presence of synapticula results in a similar encroachment on the outer regions of *Siderastræa*, at the same time leading to a disappearance of the peripheral portion of the mesenteries (Pl. XXII).

The extent to which the gastro-cœlomic cavity may be prolonged over the edge of the calicinal wall, before it terminates at the line of communication with the adjacent polyps, varies greatly in different species. In the older regions of colonies of *Oculina*, the interval between one polyp and the next may be a centimeter or more; the mesenteries may, however, cease before the spiral line of union of contiguous polyps is reached. In *Cladocora* the outside of the theca may be covered for 5 or 6 mm. by the fleshy tissues, and the mesenteries subdivide the inclosed chamber for practically the whole distance (Pl. VII, fig. 54). The calicinal wall in *Orbicella* and *Solenastræa* is prolonged but a short distance above the level at which the contiguous polyps are united with one another. Just as the calicular portion of the polypal cavity is partitioned and intruded upon by skeletal growths, so is the narrower extracalicular space; the mesenterial continuations divide it into vertical chambers, and costal ingrowths usually alternate with the mesenteries, corresponding with the septa internally. In *Madrepora*, where no perithecal mesenteries occur, the space is broken up by costate ridges, which are more numerous than the septa within. Here, however, the skeletal ridges actually come into contact with the superficial wall and support it, and were it not for transverse communications the perithecal cavity would be typically represented by a series of distinct vertical canals.

SYNAPTICULA.

Synapticula are solid calcareous bars of various form which unite adjacent septa across the interseptal loculus. They are formed by the enlargement of granulations on opposite faces of adjoining septa, growth continuing until the projections meet in the middle of the interseptal space and fuse, without the presence of any intervening soft tissues. Intermediate stages in the formation of indentations of the skeletotrophic walls lining the interseptal spaces are presented by corals in which the septa bear only granulations. The complete skeletal fusion necessarily leads to the piercing of the skeletotrophic tissues originally covering the granulations, and by means of which the calcareous additions are made. The mesentery contained in the interseptal chamber is likewise perforated as a result of the skeletal growth across the chamber containing it.

Much discussion has arisen as to the systematic value to be assigned a synapticulum, according as it is completed by the simple enlargement of two granulations, or by the intercalation of one or more additional centers of growth. The former have been termed by Pratz (1882) "False synapticula," and the latter "True synapticula." The polypal tissues themselves show no distinction, according as one method or the other is followed, and for discussion as to their importance in skeletal morphology the works of von Koch (1896, p. 259), Ogilvie (1896, p. 184), and Vaughan (1900, p. 47) among others may be consulted.

The genus *Siderastræa* is especially favorable for a study of the relationships of the polyp to these characteristically Fungid structures (Pls. XXII, XXIII). In the corallum of *Siderastræa* the synapticula are seen as vertical rows of short, thick, nearly circular bars, stretching from one septum to another across the interseptal space, and mainly restricted to the peripheral region of each corallite.[a] Upon decalcification of a polyp the soft tissues remaining are found to be made up of a large number of radiating vertical lamellæ. In the upper region these are united centrally, but are mostly free from one another below, and all terminate at about the same level. The complete separation of the lamellæ results from the fact that in the lower region of each corallite the septa extend all the way from the calicinal wall to the central columella, and, uniting with the latter, wholly cut off one septal loculus from another. In its natural state each lamella is separated basally from the lower part of the corallum by a delicate horizontal dissepiment, exactly as in other corals, except that the dissepiment in its course may encounter the synapticula. The lamellæ thus represent the interseptal polypal tissues freed by decalcification; each consists of two lateral walls which lined adjacent septa, and above contains a single mesentery, while below it is empty.

A surface view of an isolated interseptal lamella, slightly enlarged, is represented on Pl. XXII, fig. 152. The edge to the right is central in regard to the polyp. For nearly the whole of its length the lamella is perforated toward its peripheral border by three rows of round or oval apertures. Smaller lamellæ may bear only two rows of perforations, while again there may be four more or less complete rows in some of the larger polyps. The apertures in the lamellæ represent the spaces which before decalcification were pierced by the skeletal synapticula, and in each corallite the increase takes place above and centrally.

Various sections of polyps of *S. siderea* are represented on Pl. XXIII, and from these the relations of the fully formed synapticulum to the polyp as a whole can be ascertained. In both transverse and vertical sections each interseptal chamber appears as if composed of several wholly distinct segments, the skeletal matter which separates them representing the synapticula. Some of the chambers are wholly or in part occupied by a mesentery, while others are empty; in the few instances in which the section of a chamber does not include a perforation, or rather a synapticulum, the loculus is complete from center to periphery. A consideration of the varied appearances which would result from sections at different levels through the complete lamella (fig. 152) will aid in an understanding of the appearances presented by the different interseptal chambers. The synapticula never wholly isolate any portion of the internal cavity, though they must interfere with the effectiveness of the peripheral circulation.

The sections further demonstrate that a gradual atrophy of the mesenteries takes place in the lower and peripheral parts of the polyp as these become invaded by the synapticula. In the uppermost polypal regions all the mesenteries are attached to the column wall and disk, and six pairs extend inwardly as far as the stomodæum; but a little below the level of the stomodæum the peripheral attachment becomes lost, while in the lowest sections no part of the mesenteries whatever remains.

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[a] For excellent representations of the synapticula in *Siderastræa* see Miss Ogilvie's paper, 1896, pp. 180–182.

All stages in the resorption of the lower parts of the mesenteries can be observed. Where the action is in progress the peripheral edge is free and tapering, although the mesentery was originally attached by this to the wall (fig. 158). The mesoglœa is seen to break up into distinct pieces, and the endodermal epithelium is in different stages of disorganization: terminal fragments appear as if about to break off, and occasionally free particles are met with. The mesenterial débris thus set free is evidently injested by the endodermal epithelium lining the chambers, for the layer is here of exceptional thickness and the large cells are crowded with granules and irregular fragments, which closely recall those given off from the disintegrating mesentery.

Fig. 153, taken from a retracted polyp, reveals that the mesenteries do not extend as far as the most peripheral chambers, although the region represented is no lower than the stomodæum. In some cases a fragment of the mesentery may persist in the second chamber, but its imperfect character indicates that it is about to disappear; even where the section does not actually encounter a synapticular interruption the peripheral tissue is atrophied.

In the tangential section, fig. 156, the mesenteries all extend vertically beyond the first transverse rows of synapticula, but in the chambers below they begin to exhibit the various stages in absorption.

That the mesenteries are actually pierced by the synapticular formations is manifest from the preparations. When serial sections are passed in review, it is seen that the mesentery wholly surrounds the upper and more central perforations left by the removal of the synapticula, and frequently the mesenterial mesoglœa becomes swollen, and presents striated areas, such as are formed by the desmocytes where a mesentery is inserted on the calicular wall (fig. 157).

Miss Ogilvie has attributed an altogether different origin to the synapticula, in her account of these structures in *Fungia* and *Siderastræa*. Commenting (p. 170) upon Bourne's description of the synapticula in *Fungia*, she states: "The important point is that they *neither 'interrupt' nor 'pierce' the mesenteries*." Further, it is assumed all along that the body wall is specially invaginated from below to produce them[a]. Had an examination of the actual polypal tissues been made it is impossible to see how any support could have been adduced for such statements, any more than would be forthcoming for the production of simple tubercles on the septa.

Professor Bourne, in his paper, "The Anatomy of the Madreporarian coral *Fungia*" (1887), also describes somewhat similar mesenterial relationships in the genus *Fungia*, only here the synapticula are in single vertical or oblique bars, not in vertical rows, as in *Siderastræa*. In the upper regions of the interseptal chambers there are no synapticula, and the mesenteries are free to radiate across the whole space between the stomodæum and the periphery of the disk, but in the lower portions of the loculi the continuity of the mesenteries becomes interrupted by the synapticula. Owing to the much larger number of vertical bars across the broad septa of *Fungia*, the intersynapticular cavities in sections greatly outnumber those of *Siderastræa*, and the mesenteries do not extend wholly across any segment, being represented by a small projection at each extremity of the chamber (Bourne's figs. 13, 15). Bourne's explanation (1887, p. 19) of the significance of the synapticula, that "physiologically they seem to serve as stays or buttresses, giving solidity and coherence to the corallum," is probably the most correct of any yet offered. From the disappearance of the mesenteries below, almost *pari passu* with the development of the synapticula, the circulation of the digestive fluids and functional activity within the synapticular region becomes diminished, and it is very doubtful if, as Miss Ogilvie (p. 171) suggests, the main advantage is that "an increased endodermal surface is afforded within the visceral cavity."

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[a] Acting upon this suggestion of Miss Ogilvie, Delage and Hérouard, in their "Traité de Zoologie Concrète, Tome II, pt. 2, Les Cœlentérés," 1901, have constructed two ingenious diagrammatic figures (pl. 62, figs. 1, 2), attempting to show how the basal infolding of the soft wall of the polyp proceeds in the formation of both bar-like and lamellar synapticula. The polyps of *Siderastræa* give no support whatever for such a conception. From the interseptal lamella represented on Pl. XXII, fig. 152, it is manifest that each synapticulum is formed independently of the others, not from a continuous infolding of the basal part of the skeletogenic layer, as Ogilvie and Delage & Hérouard assume.

Where the mesenteries are pierced and fixed by synapticula it is manifest that their retractile power will be lost: hence, only centrally and above will they still be able to extend and retract. With this, perhaps, may be associated the fact that the polyps of both *Siderastræa* and *Agaricia* are able to expand above the corallum the least of any species coming under observation. Colonies of the former have been kept in aquaria for months, and the polyps raise themselves but little above the corallum.

COLUMELLA.

If the aboral surface of a coral polyp be examined after decalcification, either as a whole or by means of sections, its middle affords certain indications as to the nature of the columella. If the calcareous tissue in the center of the corallite be elevated and solid, it intrudes, as it were, into the central basal part of the polyp, just as the septa intrude radially, and upon its removal a conical chamber remains. The soft tissues of the interseptal loculi are then wholly distinct from one another, for a greater or less vertical distance from the base, and in transverse sections the loculi are separated both laterally and centrally (figs. 55, 84). The calcareous deposit in these cases extends radially from without the boundary of the polypal tissues to the central deposit. If, on the other hand, the middle of the corallite be occupied by a spongy or merely convoluted calcareous mass, irregular chambers remain, which represent so much of the gastro-cœlomic cavity of the polyp, and serve to maintain the different interseptal loculi in communication (fig. 142).

The details represented by polypal sections, however, afford no evidence as to how the columella has been produced, whether as an upgrowth of the floor of the corallite, or by fusion of the free edges of the septa, or by both combined. This can best be ascertained from an examination of the skeleton itself.

ORDER OF APPEARANCE OF SEPTA.

PROTOSEPTA.

In accordance with the division of the mesenteries into Protocnemes and Metacnemes, the septa appearing in association with them will be described as "Protosepta" and "Metasepta" respectively. The protosepta will include the six primary septa appearing within the primary entocœles, and the six septa which appear within the primary exocœles; all the succeeding septa, arising within the entocœles or exocœles of the later mesenteries, will be metasepta. The septa within the directive entocœles are known as "Directive Septa," and are axial in position. Sometimes, as in *Madrepora*, these can be distinguished from the other protosepta by their greater or less size, and thus give a marked bilateral character to the calices.

Prof. H. de Lacaze-Duthiers (1873) was the first to observe the origin of the primary septa in coral larvæ, his researches being conducted upon the simple, perforate coral, *Astroides calycularis*. The description and figures indicate that twelve independent septa appeared simultaneously, one in each mesenterial chamber, while the young polyp was at the protocnemic stage of development. Apparently from the beginning each septum was constituted of three pieces, arranged in a Y-shaped manner, the bifurcated end being peripheral. Prof. G. von Koch (1882) subsequently obtained similar results for this species, at the same time fully establishing the ectodermal origin of the skeleton. In a paper, "Evolution du Polypier du *Flabellum anthophyllum*," Lacaze-Duthiers (1894) refers to young specimens of this species with only six septa and six tentacles, and in later coralla, where twelve septa occur, the members of the second cycle are much smaller than those of the first. G. von Koch (1888) had previously demonstrated, by means of serial sections of adult coralla, that *Flabellum* at its earliest stage is provided with only six septa, and that an alternating cycle of six appears later.

In one of his last works on corals, Lacaze-Duthiers (1897) makes further important contributions to our knowledge of the early stages in the development of the septa, so far as the process can be followed by observations on the living polyp and macerated coralla. A very complete series are given, illustrating the appearance of the septa in *Balanophyllia regia*, as well as notes on those of *Caryophyllia* and other forms. The corals *Leptopsammia* and *Cladopsammia*, in addition to *Astroides* and *Balanophyllia*, were found with twelve primary septa appearing simultaneously.

Prof. G. von Koch's paper (1897), on the development of *Caryophyllia cyathus*, indicates that in this imperforate coral the six entocœlic septa are the first to appear, and are early attached to the theca, which arises a little later and independently of the septa. The alternating exocœlic septa appear somewhat later than the entocœlic, and like them are uniform in size, but shorter in their radial extent. The basal plate preceded the development of the septa, appearing at first as six independent, somewhat triangular, calcareous deposits, which afterwards fused with one another. Here, again, the protocnemes alone are developed, and only as far as the *Edwardsia*-stage, the fifth and six pairs being incomplete.

My results on the origin of the septa in the fissiparous coral *Manicina areolata*, so far as they go, coincide with those of Lacaze-Duthiers and von Koch. The septa appeared as upgrowths of the basal plate, covered on both sides by the basal wall of the polyp (fig. 137). The first six septa appeared simultaneously, within the entocœles of the larva at the *Edwardsia*-stage of mesenterial development (fig. 135): on the other hand, no exocœlic septa had arisen when the young polyps were preserved, although an interval of over a week had elapsed since the appearance of the entocœlic members. There is good reason to suppose, however, that the primary exocœlic members never appear in *Manicina*, as exocœlic septa seem to be absent from the adult.

In numerous polyps of *Siderastræa radians* reared from larvæ, the six members of the primary cycle of septa appeared simultaneously, within the six primary entocœles, three or four days after fixation of the larva, and in practically all cases were equal in size. Each septum was at first a simple lamella, with the upper edge distinctly serrated, and the lower edge flat and adherent to the glass to which the polyp was affixed. A day or two after the formation of the first cycle of entosepta, the six exosepta began to make their appearance, in some cases practically simultaneously, but in others in successive bilateral pairs from the dorsal to the ventral aspect of the polyp (p. 492). Thus in fig. 12*c*, a septum occurs in each of the two dorsal exocœles, a rudimentary member in each middle exocœle, while in the ventral chamber no skeletal formation is yet apparent. Figs. *b*, *c*, although representing different stages, were taken from two different polyps of the same age.

The young polyps of *Siderastræa* in the end presented two complete cycles of protosepta, a primary cycle consisting of six equal entosepta, and a secondary cycle of six equal exosepta, the latter series having appeared later and remaining a little smaller than the former. The protoseptal stage was completed within the first fortnight after the extrusion of the larvæ. In the later growth of the septa the peripheral extremities assumed a Y-shape, the additional portions appearing in some instances as distinct formations, and in others as continuations of the primary simple septum.

The above examples all agree in the fact that the six entocœlic septa arise simultaneously at the developmental stage marked by the presence of six pairs of mesenteries, and with the Edwardsian mesenteries alone complete. Lacaze-Duthiers' figures of *Balanophyllia regia* indicate that when the septa appear all the twelve mesenteries are united with the stomodæum, but no microscopic sections were made to confirm this. In *Astroides*, *Balanophyllia*, and others, the exocœlic septa appear along with the entocœlic, but an interval elapses in *Caryophyllia*, *Flabellum*, and *Siderastræa* before this takes place, while in *Manicina* they are wholly wanting. Where exosepta are developed, the six members usually appear together, but in certain polyps of *S. radians* a decided dorso-ventral succession in bilateral pairs was followed.

The simultaneous appearance of the cycle or cycles of protosepta in corals, and their uniformity in size, are in marked contrast with the successive order of development followed by the pairs of protocnemes. In no case do the septa appear until the six primary pairs of mesenteries are fully established, and then the six members of the cycle arise together. The septal sequence most nearly conforms with that of the tentacular, in which the members of a complete cycle, or both inner and outer cycles, appear together.

It must be borne in mind that the protocnemes are practically established at the time the larva settles, and that no skeletal formation takes place before the sedentary stage is assumed. During the subsequent growth of the coral, the new septa (metasepta) are found to arise in a dorso-ventral succession, approximately *pari passu* with the pairs of mesenteries, and it may be conceived that if the larvæ settled with only a few pairs of mesenteries developed then the primary septa would show a corresponding succession in their appearance.

In most adult polyps of *Porites* and *Madrepora* the protoseptal stage is retained, six entocœlic members and six exocœlic forming a larger and a smaller cycle. Very often some of the twelve septa are wanting, and usually one or both of the directive septa are much larger than the lateral. thus exhibiting a bilateral symmetry, corresponding with that of the mesenteries and tentacles.

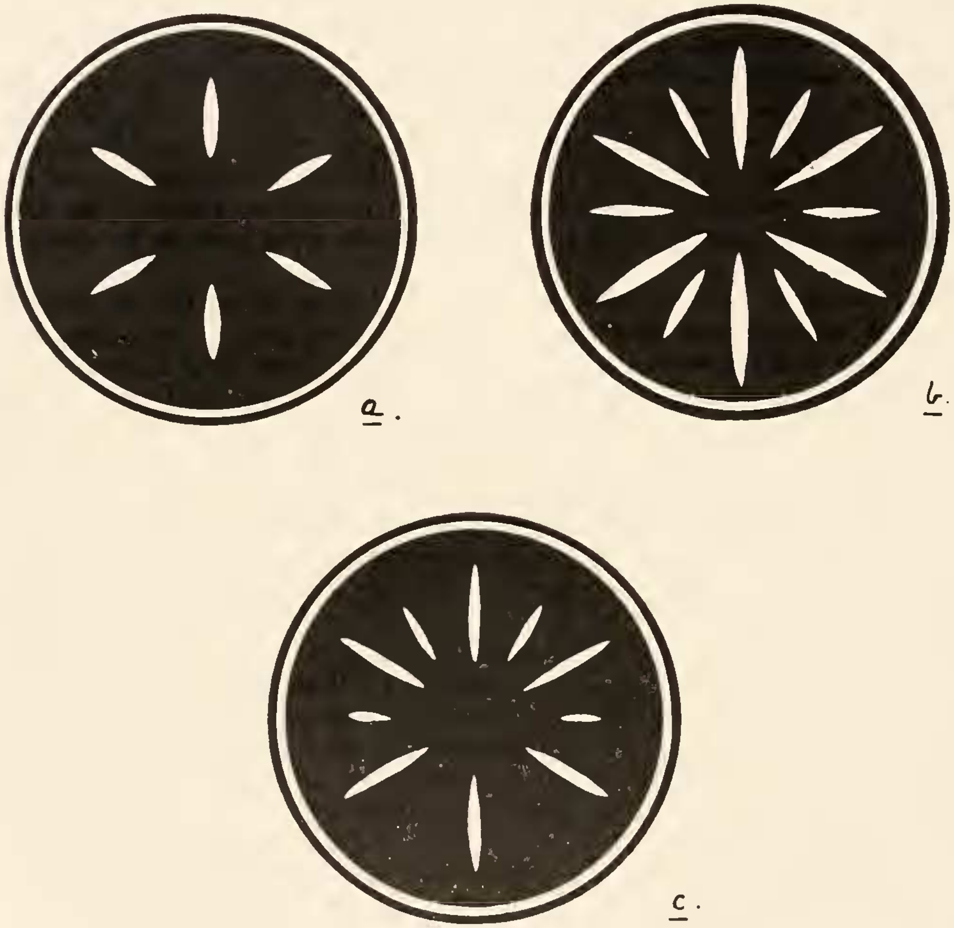

Fig. 12.

Siderastræa radians.—Series illustrating the development of the protosepta in larval polyps. The outer white ring represents the epitheca. *a*, Six equal entosepta are present, developed simultaneously. *b*, Six equal smaller exosepta now occur, also developed simultaneously, and alternating with the six primary entosepta. *c*, Successive appearance of the exosepta from the dorsal to the ventral aspect of the polyp, observed in a few cases.

The young bud of *Madrepora*, represented in section on Pl. III, proves that in asexual growth all the protocnemes may make their appearance before septal development commences, so that it seems not improbable that the protosepta may arise simultaneously in bud as well as in larval polyps.

It is manifest from the examination of buds of other genera that the septa occur in accordance with the number of the mesenteries at any particular stage, or at any rate their downward extension is in conformity with the mesenteries present. It is found that as the mesenteries disappear downward so do the septa; or conversely, as the pairs of mesenteries increase in number the septa follow. This is well shown in the series of sections of the bud of *Solenastræa* on Pl. XII. In the transverse section, represented in fig. 89, nine protocnemes are present, and the same number of alternating septa, the latter indicated by the septal invaginations. Only one representative of the incomplete fifth and sixth pairs (V) occurs at the stage, and with it is associated a smaller septum. This mesentery disappears a few sections below, and then the septa become octameral, in correspondence with the four pairs of mesenteries remaining; as others of the mesenteries disappear the septa are found to follow, and in the last section obtained (fig. 90) only six mesenteries and six septa occur.

Whatever be the arrangement of the septa in adult corals, all the evidence seems to indicate that either six or twelve protosepta constitute the fundamental plan for all Madreporaria, whether recent or extinct. Thus, by means of serial sections, Prof. G. von Koch (1889) has proved that the coral *Caryophyllia rugosa*, which Moseley (1881), from his studies of the adult, first described as octameral, is really hexameral in its early stages. At first, six septa of the primary cycle are present, then six septa of the second cycle, and it is only with the appearance of a third cycle that modifications are introduced which lead to the production of the adult octameral condition. Lacaze-Duthiers (1894) refers to the eight or ten systems of septa exhibited by *Flabellum*, yet the early stages are typically hexamerous.

Lindström's results in regard to the coral *Duncania* are also of the same character. Pourtalès (1871) regarded this in the first instance as a living member of the order Madreporaria Rugosa. With regard to the tetramerism of its septa, Lindström, as quoted by Pourtalès, writes:

"There seems to be no reason to class this species, Duncania, among the Rugosa, which commonly are considered to have four septa of the first order. In making a thin section of the apex of a Duncania I distinctly saw six septa of the first order, which met in the center."

There is also evidence, from the results of Ludwig and Pourtalès, that some of the Palæozoic Tetracoralla exhibit a like hexameral primary condition.[a]

Solenastræa hyades is hexameral as far as the third cycle of septa, but the additions beyond this take place in such a manner as to wholly destroy such symmetry. The septa of adult polyps of *Manicina* and *Favia*, which reproduce by oral fission, exhibit no hexameral plan, yet the early stages have been found to be of this type, and such can probably be assumed of fissiparous corals generally.

The instances are sufficient to show how little importance can be attached to the disposition of the septa in the adult coral, when discussing the broad relationships within the group. The whole history of any form must usually be known before its true nature can be determined, or any great importance assigned its adult peculiarities. The soft parts afford the surest guide for morphological comparison, from the greater certainty with which the relationships can be determined, owing to the many structural details available for correct orientation.

It has already been shown that, as regards the appearance of the twelve protocnemes, there is evidence of practical uniformity throughout the Actiniaria and Madreporaria; the several divergences in the later mesenterial sequence, distinguishing the great groups, make this their starting point. As regards the septa, also, there is good reason to expect that the six or twelve protosepta will be found characteristic of both living and extinct corals, and that all the numerous types of metaseptal sequence likewise make this their point of divergence. The distinctive characters of the principal divisions of the Zoantharia are not manifest from the beginning, but from the completion of the protocnemic stage.

METASEPTA.

The endeavor to establish the order of appearance of the septa beyond the primary stage presents many difficulties; no uncertainty can possibly arise as far as the protoseptal stage, but

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[a] The subject is further discussed in a paper: "Relationships of the Rugosa (Tetracoralla) to the living Zoantheæ." Johns Hopkins Univ. Circ., vol. xxi, no. 155; also, Ann. Mag. Nat. Hist., ser. 7, vol. x, May, 1902.

it is doubtful if the next step in septal development is yet fully understood. Milne Edwards and Haime (1857) first attempted with any degree of thoroughness to determine the law governing the septal sequence of corals, and gave expression to their general results in the well-known figure on Pl. A5 of the Atlas accompanying the "Historie." Their investigations, however, were conducted almost exclusively upon adult coralla, the determining factors being the comparative sizes and radial extent of the different septa. The relative size and extent of the septum were conceived to indicate the order of appearance; the largest, most developed septa, were the oldest or first formed, the smallest were the last formed.

Prof. G. von Koch, in the course of his wide and thorough studies of coral morphology, has investigated the laws governing the order of appearance of septa more fully than any other writer. His results are largely founded upon the order of appearance and relative magnitude of the septa in serial sections of fully developed coralla, a method far more likely to yield reliable results than an examination of only the superficial characters of the calice. He concludes that in the main the law of Milne Edwards and Haime expresses the actual facts of the case—a new septum always appears between two older septa, and as a rule a perfect cycle is present before the septa of the next cycle arise.

Unfortunately, there is no account available of the order of development of the first metasepta in their relation to the mesenteries, and yet it is only upon this relationship that the problem can be satisfactorily solved. Both Lacaze-Duthiers and von Koch describe such early stages in the formation of the corallum, but in no case is the relationship of the mesenteries indicated.

One of the facts frequently emphasized in the present investigations is that the formation of the septa follows very closely upon the appearance of the mesenteries. In ordinary cases, whatever be the number of mesenterial pairs present, an entoseptum and an exoseptum are associated with each. This is clearly shown in the serial sections of the young bud of *Solenastræa* (Pl. XII); the polyps of *Astrangia* (fig. 47), *Phyllangia*, and *Cladocora* (fig. 49) are also very instructive in this respect. The correspondence in the number of mesenteries and septa at all stages can be established with the greatest certainty; if any mesenterial cycle is incompletely developed so is the septal. In *Manicina* (fig. 132) and *Pectinia* septa appear as a rule only within the entocœlic chambers, but one corresponds with even the youngest of the mesenterial pairs.

Transverse sections of *Manicina* sometimes reveal septal invaginations within the exocœlic chambers, as in fig. 132, although by far the majority are entosepta. On following the sections toward the distal region, however, mesenterial pairs are usually encountered which correspond with the apparent exocœlic septa seen below. Thus the latter are really entosepta which in their downward growth exceed that of the mesenterial pair within whose interspace they occur. H. V. Wilson (1888) states that the septa of *Manicina* may for a time be exocœlic, but it is doubtful if higher sections would not have revealed the corresponding mesenteries. Bourne (1893) also found a few exocœlic septal invaginations in *Fungia*, though only entosepta are the rule; here, again, it is likely that the more distal regions of the polyp would have revealed the corresponding mesenterial pairs.

From an examination of a large number of stages in the growth of various species, it becomes manifest that the sequence of the septa beyond the protoseptal stage follows very closely that of the mesenteric succession. Knowing then the order of appearance of the mesenteries, that of the septa can be determined also. The metacnemes have been shown to appear, not a cycle at a time, but in successive bilateral pairs from one aspect of the polyp to the other, and the septa must follow a like sequence. Although in the end the mesenteries and septa of any one cycle become practically equal in size, yet the early stages render it evident that adult size does not conform with order of appearance.

A difficulty arises, however, in connection with the exosepta. It has been established throughout that the exosepta, like the exotentacles, always constitute the last or outermost cycle; the entosepta form all the internal cycles, the sum of the entosepta corresponding with that of the exosepta. But at all stages in the development of most corals, from the protoseptal stage onwards, exosepta occur. The important question therefore arises, whether the exosepta of the early stages become the entosepta of the later or adult stage, or whether the exosepta remain exosepta throughout their existence. It is clear that whichever method is followed will lead to very different fundamental results in formulating the law of septal sequence.

The former condition appears to be very generally assumed. According to this, the six primary exosepta are considered to represent the second order of entosepta found in the developing coral in which the primary and secondary orders of mesenteries have appeared. The outermost cycle of twelve septa, constituting the third cycle, would be exosepta, and represent new formations, alternating with the twelve older septa. The twelve pairs of tertiary mesenteries on their appearance would include these third-cycle septa within their entocœles, and thus the exosepta of a previous stage would become the entosepta of a later stage. The next cycle of septa would consist of twenty-four exocœlic members alternating with the first, second, and third cycles, and on the appearance of the quaternary mesenteries these would likewise become entosepta, followed by a fifth cycle comprising only exosepta.

My investigations so far give support to the view that the exosepta remain exosepta throughout, and that new entosepta arise with the new pairs of mesenteries. The results, however, are not yet sufficiently complete to fully establish the method. Such a relationship agrees with what actually takes place during the growth of the different cycles of tentacles; an exotentacle remains an exotentacle throughout the life of the polyp, those appearing early being displaced by the later entotentacles.

ASEXUAL REPRODUCTION.

By far the majority of corals are colonial in habit, and in nearly all cases the colony is produced as a result of the non-sexual or vegetative reproduction of an original, sexually-formed, simple polyp. It follows that in any study of the Madreporaria much attention must necessarily be given to the various methods of polypal increase other than by larvæ.

Some few instances are known in which colonies are formed by the direct union or aggregation of individuals originally distinct. For these G. von Koch (1890, p. 376) employs the term "Aggregated Colonies," to distinguish them from colonies produced by the budding or fission of a single polyp. Von Koch describes such aggregated colonies in the usually simple coral, *Balanophyllia verrucaria*, and shows that in all probability they have been produced from originally free and distinct larvæ which settled near one another, their skeletons afterwards becoming fused in a common deposit. Lacaze-Duthiers (1899) describes the production of somewhat similar aggregations, "boquets," in certain specimens of *Caryophyllia* obtained from Port Vendres. In the process of fixation of the larvæ of *Siderastræa radians* I have actually observed such aggregations taking place, and have followed the formation of colonies therefrom as far as the production of the tentacles and early stages in the appearance of the skeleton.[a]

The foregoing, however, are only exceptional instances of colony formation, and need not be further noticed in any general consideration of the subject.

The manner in which polypal increase is brought about, whether by budding, or by fission, or both combined, varies greatly in different species, and is the main cause of the immense variety of form assumed by colonial corals. So far as the resulting types of growth can be studied by observation of the skeleton alone, they have been described by writers such as Dana, Milne Edwards and Haime, and Duncan, and an extensive terminology has arisen in connection therewith. Dr. A. Ortmann (1890), in his paper "Die Morphologie des Skelettes der Steinkorallen in Beziehung zur Koloniebildung," has summarized the methods of colony formation in a very detailed manner, and at the close of the account applies the results in part toward a classification of the Madreporaria. Von Koch, in various contributions, has also given much attention to the process of coral budding, especially as revealed by means of serial sections of the corallum. As the earliest stages in the production of any new polyp must necessarily take place within the soft tissues of the parent, the study of these should yield results of fundamental importance.

So far as the species of corals under observation are concerned, all the methods of asexual polypal reproduction can be reduced to two types, which result in very different morphological

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[a] "Aggregated Colonies in Madreporarian Corals." Amer. Nat., vol. xxxvi, 1902.

conditions. I recognize vegetative growth only by *budding* and by *fission*. The differences manifested within each division are mainly such as are dependent upon the position and method according to which the process takes place, and these do not in any way modify the essential distinctions between the two types.

When studying the mesenteries of adult polyps, two great divisions were determinable. In one section, including the genera *Orbicella*, *Solenastræa*, *Oculina*, *Cladocora*, *Astrangia*, *Phyllangia*, and *Siderastræa*, the mesenteries of all the polyps in a colony were found to be arranged according to the regular, hexameral, cyclic plan, with two pairs of directives; while in the other section, embracing the genera *Favia*, *Dichocœnia*, *Isophyllia*, *Manicina*, *Mæandrina*, and *Colpophyllia*, the mesenteries have lost their hexameral cyclic regularity, including the directives, and little more than a distinction into complete and incomplete pairs can be established. It was further found that the first-mentioned group comprises genera whose asexual growth is by gemmation, while fissiparity is characteristic of the latter. In whatever position the buds are produced, whether on the disk, upper part of column wall, intercalary, marginal, apical, cœnosarcal, or stolonic, matters not; the polyps retain a hexameral disposition of the organs. Also, whether the products of fission assume an individuality, or remain as constituents of a complicated system, makes little difference as regards the irregularity of the arrangement of the mesenteries, tentacles, and septa.

This fundamental difference in the adult polyps of the two groups seems to be determined by the fact that in gemmation the polyp as a whole is formed practically as a new individual, whereas, in fissiparity, some parts at least of the essential organs of the new polyp are obtained fully formed from a parent polyp. In the one case the polyp as a whole is free to develop according to a definite plan characteristic of the species, while in the other new organs are to be added and adapted to parts already formed, and fissiparity may again take place before any second regularity has been established. Growth in the one is altogether new, and in the other it is patchwork—some regions new, some regions old.

It has not been possible to determine whether in every case of gemmation the mesenteries are formed wholly independent of those of the parent. In some instances they certainly are, and in others it seems very probable. In very young buds the mesenteries are already found to be wholly cut off from those of adjacent polyps, and the bud is free to develop as symmetrically as any sexually-produced polyp.

Either one or the other method of growth is in the main characteristic of any species; sometimes a case of simple fissiparity may be found in a species where gemmation prevails,[a] as in *Madrepora* and *Porites*, but the converse has never been found—that is, the production of buds where fissiparity is the rule.

Intermediate stages are not wanting which seem to indicate how the passage from the one mode of colonial growth to the other has been brought about. In corals like *Cladocora* and *Oculina* the buds usually arise toward the upper extremity of the column wall, and it is easy to understand how gemmation may overstep, as it were, the usual boundary and occur on the discal wall. Such apparently happens, for occasionally polyps of *C. arbuscula* and *O. diffusa* are found in which two oral apertures are inclosed within one system of tentacles, and a common column wall and theca occur. In such cases the two polyps may be equal, or one may be larger than the other. Microscopic examination of these shows that the normal hexameral regularity of one of the polyps, along with the presence of two pairs of directives, has in no way been disturbed, and the other polyp is either perfectly hexameral, or evidently on the way to become so. Such double polyps can certainly not be regarded as fission products, at any rate not according to the plan followed where fissiparity prevails. They seem best understood as discal buds, or as examples of fissiparous gemmation (see foot-note).

It is but one step from discal budding to oral fission, or perhaps the conception may be

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[a] The occasional instances of simple fission in corals reproducing by gemmation have since been found to be a modified form of budding, which I have termed "Fissiparous Gemmation"; the products are altogether different from those in ordinary fissiparous growth, being cyclical, hexamerous polyps, with two pairs of directives. This discovery greatly strengthens the separation between the two groups of corals. "Morphology of the Madreporaria.—IV. Fissiparous Gemmation." Ann. Mag. Nat. Hist. (In press.)

simplified by regarding the latter as stomodæal budding; but, as already stated, the step involves an important morphological distinction. Although the stages in division of the mouth or stomodæum have not been actually observed, the results to be detailed below prove conclusively that in fission the stomodæal wall is actually divided into two equal or unequal parts, and that the complete mesenteries inserted on each part go along with it, and help to form the new or daughter polyp. The plane of fission is entocœlic, and usually at right angles to the directive plane and longer oral axis; hence, only one pair of directives is retained by each of the two primary daughter polyps (p. 505). Were fission to proceed no further in all probability the mesenteries in their later growth would assume the hexameral plan, and the polyps would only differ from a larval or bud polyp in having but one pair of directives. In most instances, however, the daughter fission polyps are again subjected to fission, so that they never attain a truly regular cyclic character.

The process of polypal gemmation and fissiparity, as revealed by individual species, will be briefly described. *Madrepora*, *Solenastræa*, and *Cladocora* will serve as examples of the former, and *Manicina* and *Favia* as illustrations of the latter phenomenon.

BUDDING IN MADREPORA.

Madrepora is a favorable form on which to study extratentacular gemmation, in a region in which there is no perithecal continuation of the mesenteries (cœnosarc). The early stages are reproduced on Pl. III, figs. 22–27, taken from longitudinal sections of a very young bud, a little below the apex of a branch.

All the sections represented are from the left side of the median axis of the bud, but the sections on the other side exhibit the same details. The right end is upper in relation to the axis of the branch on which the bud was situated, and the left end is lower. Fig. 22 is from the median dorso-ventral plane passing through the stomodæum and the axial entocœles. The polyp is yet scarcely raised above the general surface of the cœnosarc; the ridges above and below (right and left in figure) probably indicate the commencement of the axial entocœlic tentacles, and the included depression the central part of the oral disk. Compared with that of the colony generally, no histological difference is yet presented by the outer ectoderm. Communication between the exterior and the superficial canal system has just been definitely established, the mesoglœa of the cœnosarc passing directly into that of the stomodæal wall. The stomodæal walls hang freely within a superficial longitudinal canal, differing in no important respect from the others around; but as the sections are taken in a longitudinal direction, the canals appear much longer than in the case of transverse sections (Pl. I, figs. 2–6). The endoderm of the canal has undergone a marked alteration from that lining the canals and gastric cavity of the polyps. It is broader, more strongly ciliated, non-vacuolated, and zooxanthellæ are practically absent, though present in the surrounding canals; long, narrow, supporting cells, with abundant protoplasmic contents, are the chief constituents. As best shown in figs. 23 and 24, the endoderm of the canal becomes thinner and more normal toward the periphery of the chamber; the inner and outer layers—ectoderm and endoderm—of the stomodæal walls are histologically alike.

The stomodæal wall for a few sections beyond that represented in fig. 22 appears as a projection from the superficial wall of the colony, hanging freely within the canal; the periphery of the projection exhibits four vertical mesoglœal strands, connected with a lower transverse strand. Later, as shown in fig. 23, three central cavities appear and separate the ridges into four distinct components. The lower transverse connecting strand is the horizontal continuation of the stomodæal wall, and the vertical strands represent the mesenteries, not yet separated from one another. The stomodæal wall is continued, as it were, along the free edges of the mesenteries, as often happens in adult polyps. In the next section, fig. 24, the upper and lower (right and left) projections have become free, but the two inner are still united by the stomodæal prolongation.

The two inner mesenteries afterwards, fig. 25, become free, and now the uppermost of the four is united with the boundary layer of the canal, and in the later sections ceases to exist. Immediately below the uppermost mesentery is a slight projection of the cœnosarcal endoderm surrounding a mesoglœal axis, which represents a rudimentary mesentery; and a few sections beyond, another rudimentary mesentery is revealed. Thus the six mesenteries of one side of the adult polyp of *Madrepora* are accounted for, four large and two small. The upper and lowermost of the four complete mesenteries now begin to diminish in size, and in fig. 26 have disappeared at the place at which the skeletotrophic layer of the canal is united with the cœnosarc; the uppermost of the two rudimentary mesenteries has likewise passed away. There now remain only the two middle mesenteries of the larger four, and the lower of the rudimentary two, and of the former, the upper is much larger than the lower. The difference is more marked in fig. 27, where the lower mesentery is disappearing, again at the union of the skeletotrophic layer with the superficial wall; the rudimentary mesentery has already disappeared. A little later, the remaining mesentery has united with the skeletotrophic layer, and is soon lost in sections beyond.

The series of sections illustrates, in the clearest manner, that buds of *Madrepora* arise along the superficial wall of a simple external canal, independently of any structural connection with the other polyps, though in communication with them by means of the canal system. The six pairs of mesenteries are fully established before the tentacles appear, and the septa are as yet wholly unrepresented. The rudimentary stage of the bud as a whole would indicate that very little time elapses between the development of the different pairs of mesenteries, if, indeed, they do not appear simultaneously. Four of the pairs of mesenteries unite early with the stomodæum, probably originating along with it; the two remaining pairs are independent of the stomodæum throughout. The complete and incomplete nature of the mesenteries thus early indicated is retained in the adult polyp; for a short distance the four larger complete mesenteries are already united with the skeletotrophic tissues, but the others have a free course from beginning to end.

The musculature at this stage is too rudimentary to afford any assistance in determining which are the directive mesenteries. But comparing the arrangement with that in transverse sections of *Madrepora* (Pl. I), there can be no doubt that the four pairs of mesenteries inserted on the stomodæum represent the eight complete mesenteries, which in the adult extend along the stomodæum, and that the two pairs of rudimentary mesenteries correspond with the free pairs, V and VI, of the adult. The outer mesenteries, right and left, will be the directives III and IV, and the two inner pairs, I and II, will be the first and second bilateral pairs. The right end of the sections being upper or axial, and the left end lower or abaxial, in relation to the colony, it is clear that the axial-abaxial relations of the complete and incomplete mesenteries are exactly as in an adult polyp.

Each of the complete mesenteries, on becoming free from the stomodæum, is somewhat club-shaped in section, but no sharp distinction yet exists between the filamental portion and the epithelium along each face, or, indeed, from the endoderm of the outer wall generally. On Pl. II, fig. 20, is represented the mesentery from another bud, at a somewhat later stage, showing the early development of the filament. The terminal region stains a little more deeply than the lateral, owing to the greater closeness of the cells, and consequent greater number of nuclei, but the tissue passes into that of the mesenterial endoderm by an insensible gradation. The gland cells and nematoblasts, characteristic of the adult filament, are not yet distinguishable.

The strong ciliation of the whole endoderm in the bud, in the earliest stages of development, is probably to be associated with the greater need of bringing an extra supply of nutrient fluid to the rapidly growing parts, while as yet the polyp is unable to take in food for itself through the oral aperture. It is only later, when direct communication with the exterior has been established for some time, that the different polypal functions become more restricted to special regions, and these exhibit corresponding histological modifications.

The subsequent development of the *Madrepora* bud takes place by an upward growth beyond the general surface of the colony. In radial polyps the lower (sulcular) region grows more rapidly than the upper (sulcar), so that the former comes to lie outside and the latter on the inside in regard to the axis of the branch. In this way the axial and abaxial relations are established.

Dr. G. H. Fowler (1887, p. 12) has contributed some brief notes upon the budding of *Madrepora aspera* (Dana), founded upon an examination of the soft tissues of the developing polyps at the apex of the branches, while G. von Koch, in his paper "Die ungeschlechtliche Vermehrung (Knospung und Stockbildung) von Madrepora," 1893, has made an important study of the same subject, but more particularly with regard to the skeleton. The short account of Fowler indicates that the stomodæum is invaginated to a considerable depth into the future polyp cavity before it is perforated, and also apparently before any mesenteries arise. The first mesenteries, already bearing filaments, are formed from the walls of the canals, apparently independently of the rest of the polyp, the connection with the stomodæum being established later. The process of gemmation in Fowler's species is thus altogether different from that in the West Indian *Madrepora*.

Many attempts have been made to obtain the early stages in the gemmation of *Porites*, but without any material results. Sections through polyps with six or eight tentacles show a corresponding number of complete mesenteries, but the remaining members necessary to make up the normal six pairs are also present, though not developed to the same degree as in older polyps. It may be that in *Porites*, as in *Madrepora*, the full complement of twelve protocnemes is produced at a very early stage and before the tentacles make their appearance.

BUDDING IN SOLENASTRÆA.

Among Astræan colonies, such as *Orbicella* and *Solenastræa*, new polyps may be either intercalary or marginal in origin. By means of the latter the colony spreads laterally, while the intercalary buds serve to occupy the larger superficial area as the colony rises in height.

The earliest marginal buds observable in colonies of *Solenastræa* are already separated from adjacent polyps on the inner side by an external groove, while the outer side, forming the periphery of the colony, is necessarily independent of other polyps. Sections made through one of these marginal buds, preserved in the expanded condition, reveal at different levels the details represented on Pl. XII, figs. 86–90.

Through the transparent tissues eight perfect mesenteries were seen to be already developed, but no tentacles were yet apparent. Fig. 86 is from a transverse section through the free stomodæal region of the column wall. All the protocnemes are present, but only the eight Edwardsian mesenteries are yet complete, while in the exocœle on each side of the dorsal directives the rudiments of a pair of second-cycle mesenteries (A, A) are visible.

The section represented in fig. 87 reveals the conditions at the level at which the bud is connected with the mother polyp on the inner side, but is free on its outer aspect; from the arrangement of the mesenteries the outer side is seen to be the sulcar or ventral aspect, and the inner the sulcular or dorsal border. The eight Edwardsian mesenteries alone bear mesenterial filaments, and the retractor muscles are sufficiently well developed to enable the pairs of directives to be determined. The pairs of metacnemes within the sulculo-lateral exocœles are better developed than in the previous figure, and another pair (B) has appeared in the left middle lateral exocœle, but the corresponding pair on the right side is undeveloped, and at this stage mesentery V has nearly disappeared on the same side. The boundary wall between the bud and the fully developed polyp is perforated in a number of places, and by this means communication between the gastro-cœlomic cavity of each is permitted. The portions of the skeleton of the adult polyp, added on the upper part of the section, represent the exsert septa, the polyp being in an expanded condition; the entocœlic septa are large and the exocœlic small. No continuity between the mesenteries of the bud of the adult polyp are represented in this or any of the sections. To the right, at the angle between the wall of the bud and the adjacent polyp, are the first indications of another bud.

Fig. 88 is taken from the region of the polyp wholly embedded in the corallum, except for a limited area on the right upper side; the bud polyp is now entirely separated from that adjacent. On the right upper side of the directive axis the fifth and sixth protocnemes, incomplete from the beginning, have now disappeared, as is also the case with the pair of metacnemes on the same side. Mesenterial filaments are no longer present on the dorsal directives (IV, IV), and the pair of metacnemes has also disappeared from the middle exocœle on the left side, but the dorsal pair (A), though very feeble, still persists.

The arrangement of the septal ingrowths, present as yet only on the left lower side, is very instructive. The largest occur within the entocœle of the pairs of directives; two are found between the left dorsal mesentery and the mesentery of the first bilateral pair (IV–II); two between this last mesentery and the mesentery of the second bilateral pair (II–I), while only one appears between this and the left ventral directive (I–III). Three of the septal invaginations are exocœlic, the exocœle of the dorso-lateral pair of protocnemes (II, V) is provided with one, but the septum of the exocœle of the ventro-lateral pair (I, VI) is as yet undeveloped. The entocœle of the persistent pair of metacnemes (A) also contains an invagination.

In the section from a still lower region, represented in fig. 89, fully developed filaments are retained only on the first three bilateral pairs of protocnemes. Only nine mesenteries are present, the mesentery remaining in addition to the Edwardsian mesenteries is the fifth member of the left side. A septum occupies each chamber between any two mesenteries, whether the two constitute a pair or not; the septum in the entocœle of the left dorso-lateral pair is small, and soon disappears along with mesentery V. The skeletal fragments within the middle of the gastro-cœlomic cavity represent the first appearance of the columellar projections.

In fig. 90 only mere traces of six of the mesenteries persist, the first pair being the strongest; the number of septa is also six, corresponding with the number of mesenteries. With one exception the septa are all united in the middle, otherwise the gastro-cœlomic cavity is divided into as many separate chambers as there are septa.

Another bud of about the same age presents a different condition with regard to the appearance of the first two pairs of metacnemes from that just described (fig. 82). The protocnemes are at the *Edwardsia*-stage, and within each of the median lateral exocœles are the rudiments of a bilateral pair of metacnemes (A, A), which are somewhat better developed in sections below the stomodæum.

The tentacles in the bud have already appeared, and exhibit an interesting stage. Fig. 83 is taken from a slightly oblique section, the upper half through the free portion of the tentacles, and the lower through their attachment to the periphery of the disk. The polyp was expanded to such a degree that the peristome projected in a cone-like manner beyond the zone of tentacles, and, as seen in the middle of the section, the Edwardsian mesentaries extend as far as the stomodæal walls. Ten of the tentacles show a regular alternation of large and small members, and, superposing the section on that in fig. 82, the tentacles arising from the entocœles are seen to be the larger, and those from the exocœles the smaller. In place of the single median lateral prototentacle on each side are three tentacles, as yet incompletely formed. These will be found to correspond in position with the incipient pair of metacnemes in the median lateral exocœles, and serve to establish that the metatentacles arise practically simultaneously with the metacnemes, an entocœlic and an exocœlic member together.

A third bud, somewhat older than either of the two described, was also studied, and the details of its lower region are represented on Pl. XIII, fig. 91. The upper right side is the border toward the centre of the colony, and the lower left side is the outer aspect. The relationships of the mesenteries, as before, show the inner border to be the sulcular aspect, and the outer border the sulcar. In the stomodæal area six pairs of protocnemes and six pairs of metacnemes occur, and of the former all the pairs are complete on one side, but the members of the fifth and sixth pairs are incomplete on the other side.

In the region represented only four pairs of the metacnemes occur, the two pairs on the upper left side having disappeared some distance above. Mesenterial filaments occur on the Edwardsian mesenteries, but not on the fifth and sixth bilateral pairs; and septal invaginations, both entocœlic and exocœlic, appear within practically all the mesenterial spaces.

The lower sections demonstrate the same relation as in the previous bud, namely, that as the mesenteries disappear, so do the corresponding septal invaginations; the metacnemes disappear first in unilateral pairs, the protocnemes in bilateral pairs. In the anterior part of the section is seen the beginning of another polyp.

Two somewhat older buds sectionized presented the following conditions: In one only ten pairs of mesenteries were developed, five complete and five incomplete, in regular alternation; in the other eleven pairs occurred, six complete and five incomplete.

The results thus briefly indicated may be summarized:

(1) The polyps of *Solenastræa*, produced asexually by gemmation, pass through the *Edwardsia*-stage of mesenterial development, in which four pairs of the protocnemes are complete and two pairs incomplete, just as in larval polyps.

(2) The metacnemes begin to make their appearance before this stage is passed over, that is, before the union of the fifth and sixth pairs of protocnemes with the stomodæum takes place.

(3) The first metacnemes appear along the polypal wall, at about the level of the inner termination of the stomodæum, as isocnemic pairs within the dorsal or sulcular primary exocœles, but in one case within the median lateral exocœles.

(4) In relation to the colony as a whole the dorsal or sulcular side is inner (axial), and the ventral or sulcar outer (abaxial). The succession of the metacnemes is therefore dorso-ventral, antero-posterior, or from the axial to the abaxial side of the bud.

(5) The mesenterial filaments and mesenteries disappear below inversely as the order of their development: first, the metacnemes in unilateral pairs, then the protocnemes in bilateral pairs.

(6) In the same transverse section the growth on one side of a polyp may be slightly in advance of the growth on the other side.

(7) The metasepta and metatentacles, both entocœlic and exocœlic, arise practically *pari passu* with the mesenteries.

BUDDING IN CLADOCORA.

The young buds in *Cladocora arbuscula* generally occur singly toward the upper part of the column wall of the terminal polyp of the sub-colonies. What seems to be discal budding has also been found to take place, when both the parent and daughter polyps are surrounded by a continuous system of tentacles and a single column wall; but the extratentacular buds seem rarely to arise above the level of the corallite. The reproductive power of any polyp is very limited, for as a rule not more than three or four polyps are connected in a sub-colony, and among these is rarely more than one immature example. Each polyp in its turn may give rise to buds, either before or after becoming distinct from the rest of the sub-colony. At a very early stage the growth of the lower abaxial aspect of the bud is in advance of the upper or axial aspect, thus giving rise to the obliquity of the polyps to one another.

Numerous extratentacular buds of slightly different sizes have been studied, and in most specimens eight complete and four incomplete mesenteries are already present, their arrangement and musculature agreeing with that of the protocnemes in larvæ of the same stage. In one case the fifth and sixth developmental pairs were absent, and, following the sections downward, only four mesenteries were present a short distance below the stomodæum; then two of these disappeared; the two remaining, which represented the first developmental pair of mesenteries, were continued much farther, and bore mesenterial filaments almost to their termination. At this early stage none of the mesenteries were in any way connected with the extrathecal continuations of the mesenteries of the parent polyp, so that evidently the buds arise on the column wall quite independently of any of the other organs of the parent, as happens in *Madrepora*, and as appears to be also the case in *Solenastræa*.

Pl. VIII, fig. 61, represents a transverse section through a bud in which two pairs of metacnemes have appeared, in addition to the six pairs of protocnemes. Owing to the difference of level at which the corresponding details occur on the inner and outer surface, as a result of the obliquity of growth, it is usually impossible to obtain all that is desired in one section: the figure is therefore a combination of the inner and outer regions of sections at slightly different levels. Above the bud is a portion of the edge-zone of an adjacent polyp.

The sulco-sulcular axis is a little to the side of the axial-abaxial plane. Only the eight Edwardsian mesenteries bear mesenterial filaments, and these alone are complete. A pair of metacnemes (A) have made their appearance in the exocœle on each side of the sulcar directives; they are feebly developed, and extend for only a few sections below the termination of the stomodæum. The three septa—two entosepta and one exoseptum—already developed at the upper side of the bud are seen to be continuations of the costæ of the adjacent polyp.

Fig. 62 is taken from a bud at a somewhat later stage, preserved in a partly expanded condition, so that sections could be obtained almost independently of the skeleton. The specimen is exceptional in that only five pairs of protocnemes are present, instead of the usual six. The directives lie in the axial-abaxial plane, and development is most forward on the outer abaxial aspect of the bud. Five alternating pairs of mesenteries, belonging to the second cycle, have made their appearance within the primary exocœles, and the pairs exhibit a progressive order of development from one aspect of the polyp to the other: the two lower pairs are the largest, the musculature is well developed, and mesenterial filaments occur at their free edge; the middle pairs are smaller and without any trace of filaments, while the uppermost pair is quite rudimentary. Sections through five exsert septa are shown at the lower border, and are both entocœlic and exocœlic.

The section is of interest as indicating the tendency to irregularities in the early formation of the bud, but more particularly as exhibiting the progressive development of the metacnemes and their filaments from one side of the polyp toward the opposite side, and the appearance of both entocœlic and exocœlic septa in connection with the metacnemes, *pari passu* with the growth of the latter.

The section represented in fig. 60 is through the protruding cone-like disk of a fully expanded young polyp, and is of importance as showing that the fifth developmental pair of protocnemes may become complete in advance of the sixth pair. On the left side is seen the outwardly reflected lower edge of the stomodæum passing along the three lateral mesenteries, and the ectoderm of the stomodæum has assumed a very symmetrical form. Below the stomodæum the six pairs of protocnemes are equally developed, and the six pairs of the first cycle of metacnemes have also made their appearance.

Extratentacular gemmation in *Cladocora* proceeds therefore exactly as in *Solenastræa*, except in the one important fact, the metacnemic succession is reversed. In the latter it is from the dorsal to the ventral surface, while in the former it proceeds from the ventral to the dorsal. However, before this exceptional sequence in *Cladocora* can be regarded as established, it will be necessary to confirm it on polyps arising directly from larvæ.

Transverse sections were made through a double polyp of *Cladocora*, that is, one where two oral apertures are surrounded by only a single system of tentacles and the two polyps have only a common column wall. One polyp was normally hexamerous, having two orders of mesenteries, not much differentiated in size, and including two pairs of directives; it differs in no essential respect from a normal simple polyp. A small polyp to the left is evidently a bud which has arisen on the discal wall of an older polyp, and as yet is imperfectly developed, having only seven pairs of mesenteries, including one pair of directives. In the stomodæal region four of the pairs are complete and two incomplete.

If the sections be compared with those of the fission polyps of *Mæandrina* and *Favia* (p. 505, *et seq.*) most important distinctions are at once manifest. In the two latter a normally hexamerous polyp has become divided through the stomodæum into practically equal halves, each half having only a single pair of directives, while in *Cladocora* a new polyp is growing by the side of another, which still retains the primary arrangement of the mesenteries, including two pairs of directives.[a]

FISSION IN MANICINA.

Manicina areolata is one of the most favorable corals on which to study the process of continuous fission, on account of the readiness with which small colonies provided with only a

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[a] The morphological significance of such double polyps in *Cladocora* and other corals has since been fully discussed in a paper on "Fissiparous Gemmation." See foot-note, p. 496.

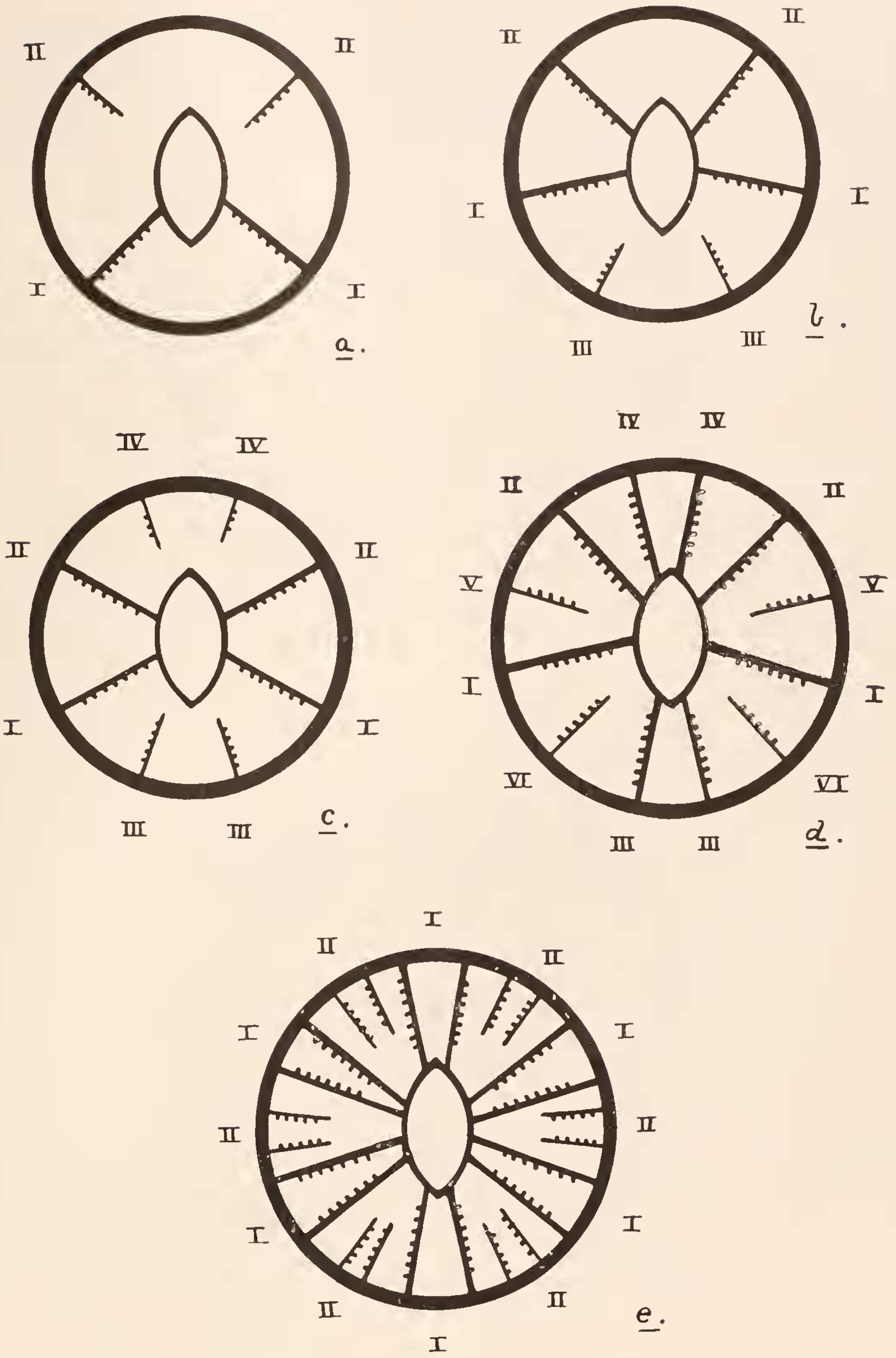

FIG. 13 (*a–e*)

Manicina areolata.—Figs. 13. Series of diagrammatic figures illustrating the mesenterial sequence in larvæ and larval polyps. *a*, *b* are taken from H. V. Wilson's (1888) account of the development of this species. *a*, Stage with two pairs of protocnemes, one pair of which is united with the stomodæum (*cf.* Wilson's fig. 18). *b*, Stage with three pairs of protocnemes, two pairs united with the stomodæum (*cf.* Wilson's fig. 27). *c*, Stage with four pairs of protocnemes (*cf.* Pl. xix, fig. 134). *d*, *Edwardsia*-stage. The larva is now fixed and remains at this stage for a considerable time, during which the six entocœlic septa are developed, and also the two cycles of tentacles (*cf* Pl. xix, fig. 135). *e*, Stage with six pairs of protocnemes, all united with the stomodæum, and the first cycle of metacnemes.

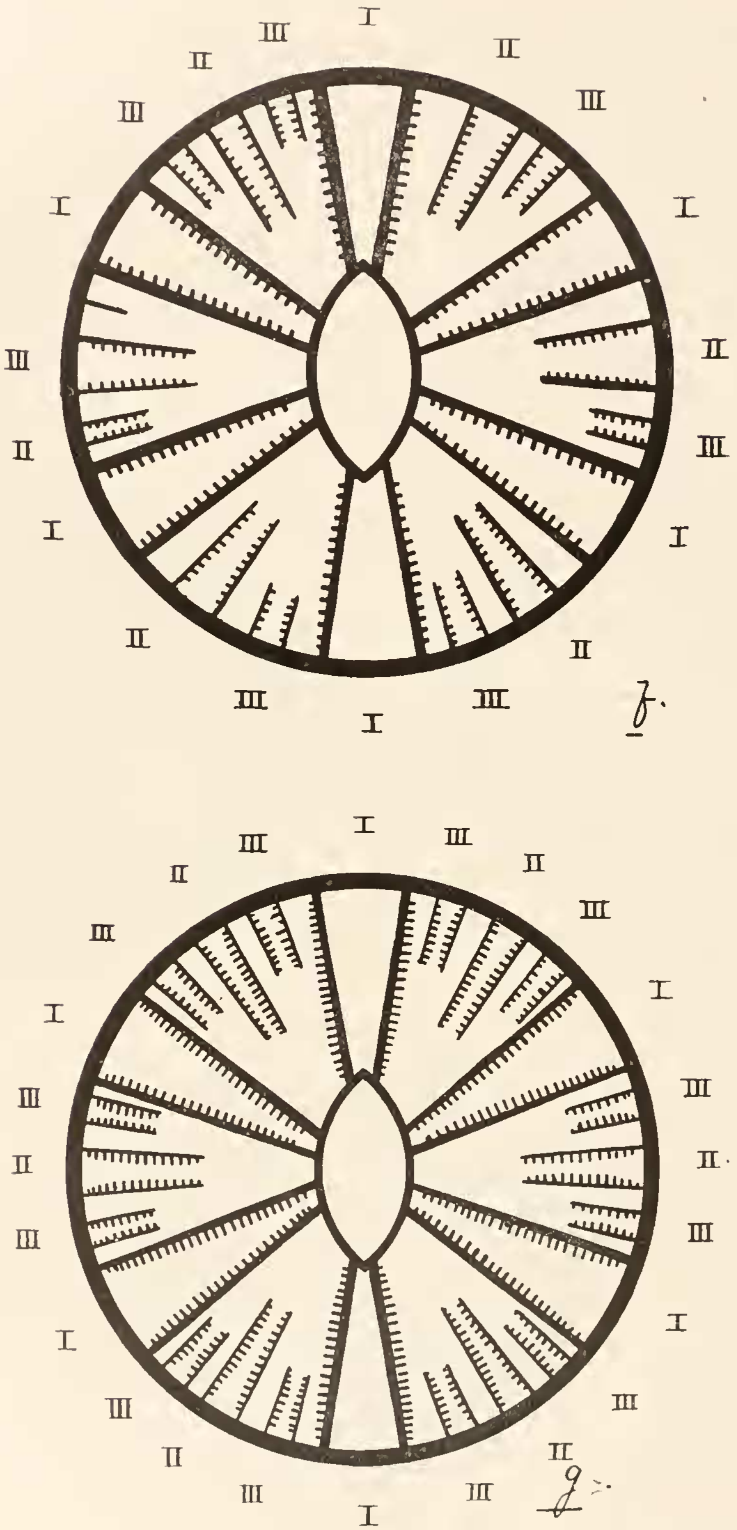

Fig. 13 (*f*, *g*).

Manicina areolata.—Mesenterial development in larval polyps continued. *f*, Seven pairs of metacnemes of the second cycle have now appeared. *g*, Stage with second cycle of twelve pairs of metacnemes complete. The young polyps now very rarely exhibit perfect regularity, the development being more advanced in some regions than in others. The members of the first cycle of metacnemes at this stage begin to unite with the stomodæum.

few oral apertures, and of a size suitable for sections, can be obtained. H. V. Wilson (1888) has traced the development of the primary mesenteries in the larvæ of this species, from the first to the sixth pairs, and has also shown that in young polyps, provided with only one oral aperture, the mesenteries are arranged in three hexamerous cycles. The first cycle comprises twelve pairs of complete mesenteries, two pairs of which are directives; the second cycle also contains twelve alternating pairs; and the third twenty-four. At this early stage the polyps of *Manicina* therefore correspond exactly, so far as regards the mesenterial arrangement, with any normal hexactinian Madreporarian or Actiniarian polyp. The diagrammatic figures on pp. 503, 504 represent most of the stages in the appearance of the mesenteries of *Manicina*. The earlier sequences have been already described (p. 450), so that attention need be directed only to the later stages, which illustrate the phenomena of fissiparity. In Kingston Harbor young polyps of *M. areolata*, with the disk bearing only one, two, or four oral apertures, are not infrequently found, fixed to older colonies of the same species, or to other corals or small pebbles.

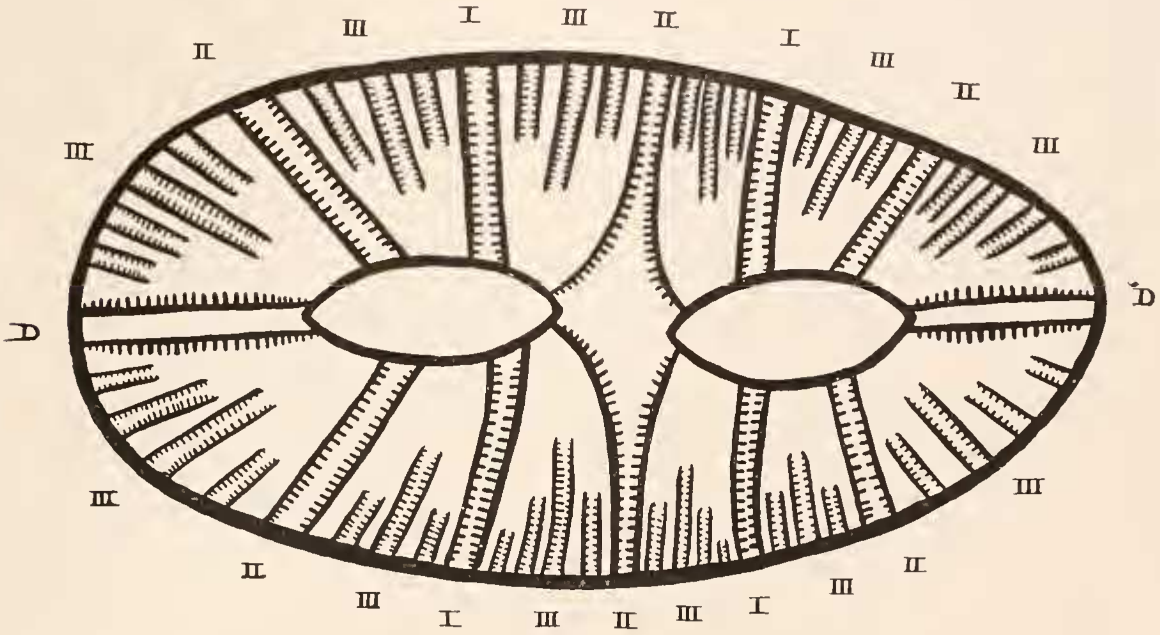

FIG. 14*a*.

Manicina areolata.—Figs. 14. Diagrammatic figures illustrating fission. *a*, Polyp with two oral apertures, twelve pairs of complete mesenteries (I, II), twelve alternating second-cycle pairs (III), twenty-four third-cycle pairs, and a few members of a fourth cycle. Associated with each stomodæum are six pairs of mesenteries, three pairs of which are protocnemes, a pair of directives being at opposite extremities. The plane of fission is within the entocœle of the middle pair of complete mesenteries on each side.

Fig. 14*a* represents the conditions in a transverse section of *Manicina* through the stomodæal region of a polyp with two oral apertures. The twelve pairs of complete mesenteries, including the two pairs of directives, represent the first and second cycles of fig. 13*g*, and comprise two alternating orders, primary and secondary, each of six mesenterial pairs; the twelve pairs of large incomplete mesenteries constitute the third order, the twenty-four next in size a fourth order, while here and there, at regions of most forward growth, occur rudimentary pairs, which are the first indications of a fifth order. The originally simple stomodæum has become divided into two, and half the complete mesenteries of the primary polyp are now associated with each stomodæum. The plane of fission passes through the entocœle of the middle lateral pair of complete mesenteries on each side, and a single pair of directives at the opposite extremities of the polyp remains attached to each stomodæum. The plane of fission is thus at right angles to the directive plane, which is also the plane including the longer oral axis of the simple polyp.

Were the separation of the disk and column wall to be completed at this stage, across the plane of fission, it is clear that two similar daughter polyps would be produced. In each case one moiety of the middle mesenterial pair of one side would form with the corresponding mesentery from the other side a pair, attached to the side of the stomodæum opposite the directives. But the longitudinal muscles of the two mesenteries in each pair would be arranged so as to face one another, instead of turning from one another, as in the case of the directives; in other words, the complete mesenteries of each polyp would include only one pair of directives, and five pairs in which the retractor muscles are vis-a-vis. The six pairs of complete mesenteries attached to each stomodæum would then constitute a first cycle, the six large alternating pairs a second, the twelve next a third cycle, and the odd pairs would represent the commencement of a fourth cycle.

The almost perfect regularity in the number, arrangement, and extent of development of the mesenteries found in the above example appears to be rather exceptional, for other specimens of *Manicina* sectionized reveal many irregularities. Fig. 14*b* represents the mesenterial arrangement in a second polyp, also bearing two oral apertures. The details are those presented by a single section toward the lower termination of each stomodæum. The hexameral regularity has been altogether lost, or perhaps was never reached. But here again the plane of fission passes through the entocœle of two opposite pairs of complete mesenteries, at right angles to the directive plane, and one of the two pairs of primary directives is found at each extremity. More than six pairs of complete mesenteries are united with each stomodæum, and only in two or three regions of the polypal wall are any members of the second and third cycles developed; the hexameral cyclic plan will be entirely lacking in the daughter polyps as in the original, and two or more complete mesenterial pairs may occur in succession, without any alternating incomplete members. In the sections higher than the one represented other pairs of small mesenteries occur, but do not in any way assist towards the production of the hexameral regularity. At the left end of the polyp two single large mesenteries occur, without any corresponding member to complete the pairs; higher sections demonstrate that one moiety has simply disappeared in advance of the other.

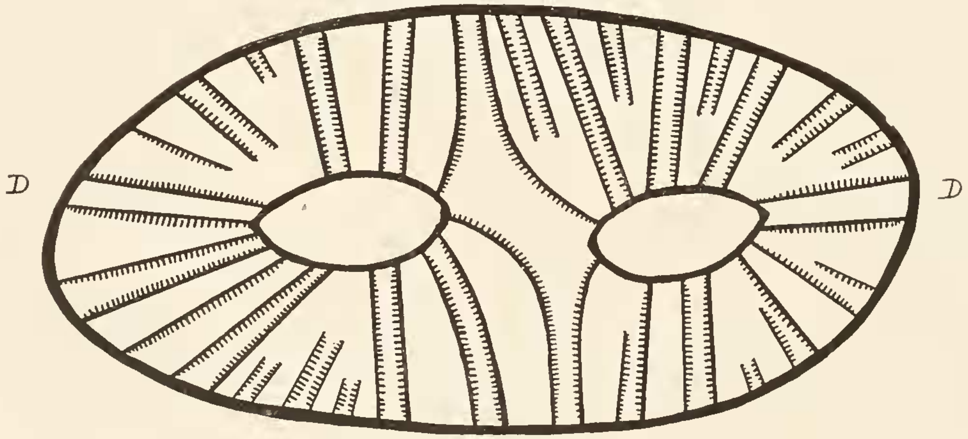

FIG 14*b*.

Manicina areolata.—Another polyp with two oral apertures. The mesenteries have entirely lost their hexameral cyclic regularity, and of the protocnemes only the directives at opposite ends can be determined with certainty.

In a third bi-oral polyp studied the alternation of first, second, and third cycles of mesenteries was a little more regular than in the last example, but was by no means perfect all round; one stomodæum was provided with six pairs of complete mesenteries, while to the other eight pairs were attached.

Young polyps of *Manicina* with three oral apertures are not so plentiful as specimens with two or four apertures. It seems not unlikely that after the first division into two, each stomodæum is again divided at about the same time, and thus the stage with three apertures would rarely occur.

Fig. 14*c* is a diagrammatic representation of the mesenteries in a *Manicina* colony with four oral apertures. The longer axis of any one stomodæum is now in a different plane from that of others, and the two primary pairs of directives are widely separated, but still situated at the opposite extremities of the colony; the two middle stomodæa have no directive mesenteries inserted on their walls. The plane of separation of each stomodæal system with one exception passes through two entocœles. The rule holds so far as the divisions on the lower side are concerned, but on the left upper side the division plane is exocœlic, a condition which is probably to be regarded as an individual irregularity.

The number of mesenteries connected with each stomodæum is inconstant; the stomodæum at the right extremity bears twelve, the next fourteen, the third twelve, while that at the left end has seventeen. The alternating incomplete pairs are still more irregular. In one or two cases they are wholly absent from the exocœle between two pairs of complete mesenteries; in many others only one pair occurs; while in a few chambers two or three pairs, representing the second and third cycles, are developed. As in the previous figure, the tendency in the older regions is toward a system of alternating incomplete and complete pairs, and only at places of most forward growth are the third and fourth cycles represented. The incomplete mesenteries further exhibit great variation in the extent of development at one and the same level; some pairs are nearly as large as the complete mesenteries, while others are rudimentary. The variability is such as to indicate that when the members of the younger orders increase in size they may ultimately unite with the stomodæum, and newer pairs appear in their exocœles. Under such circumstances it is scarcely possible to determine a cyclical plan.

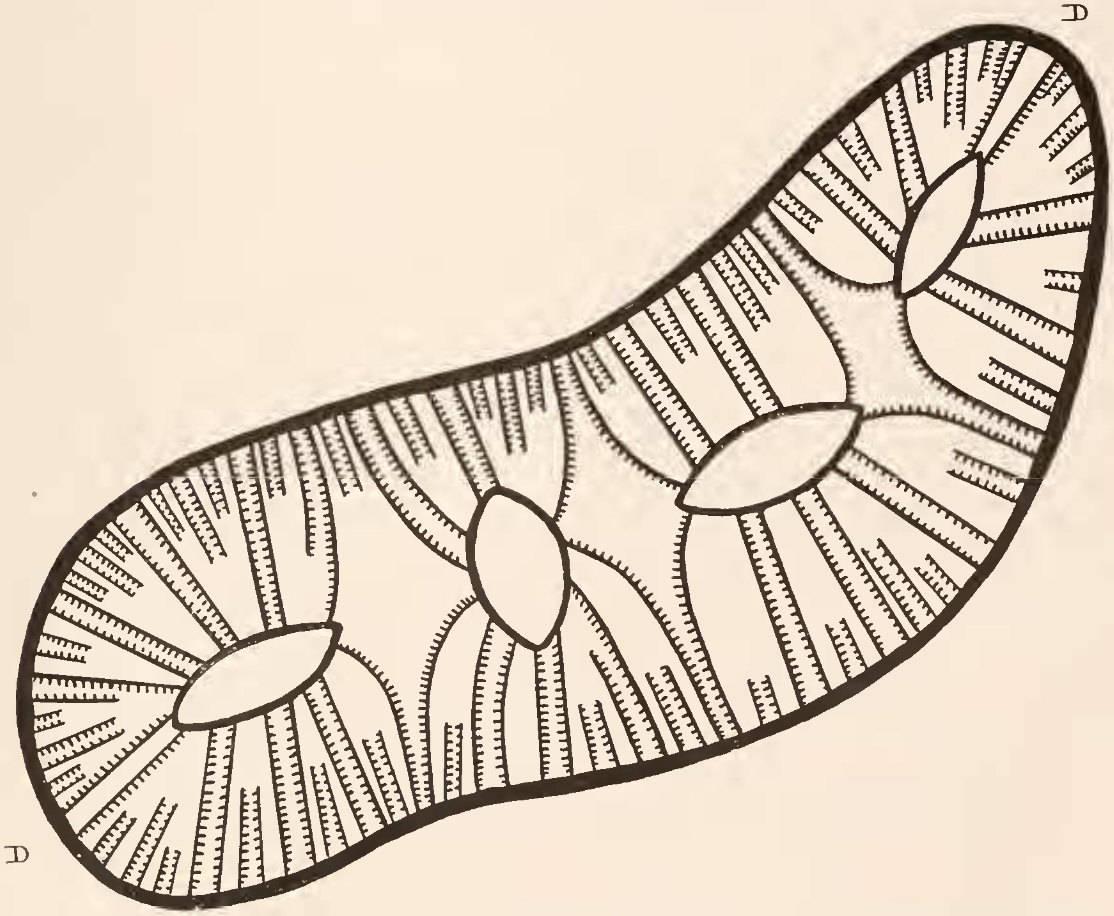

Fig. 14*c*.

Manicina areolata.—Polyp with four oral apertures. The mesenteries exhibit a tendency to an arrangement in alternate complete and incomplete pairs. The regions of most vigorous growth are at the opposite ends, where also the primary directives are still situated The fission planes are entocœlic, except for the irregularity at the upper left hand corner.

The phenomena presented by the early divisions of *Manicina* clearly prove that fission actually takes place in a plane at right angles to the long axis of the mouth and stomodæum; otherwise the regular distribution to each daughter stomodæum of six complete pairs of mesenteries, derived from the primary twelve pairs, with one pair of directives only at opposite extremities, would be inconceivable. Although among the many living colonies which have been examined, examples in which the oral aperture or stomodæum was in the actual process of division have not been observed, yet frequently two small mouths are found in close proximity, suggesting that they have arisen from the splitting of a single larger aperture.

The later divisions in *Manicina* reveal that the fission of the stomodæum, along with its associated mesenteries, is not always median, or results in the production of equal halves. Sometimes in living polyps a very small aperture will be found, as if cut off from a larger, and only a few mesenteries are associated with it compared with the number united with the latter.

FISSION IN FAVIA.

Favia fragum occurs in some abundance on the reefs throughout the West Indies, forming small, convex, hemispheroidal or irregular colonies, usually four to five centimeters in diameter.

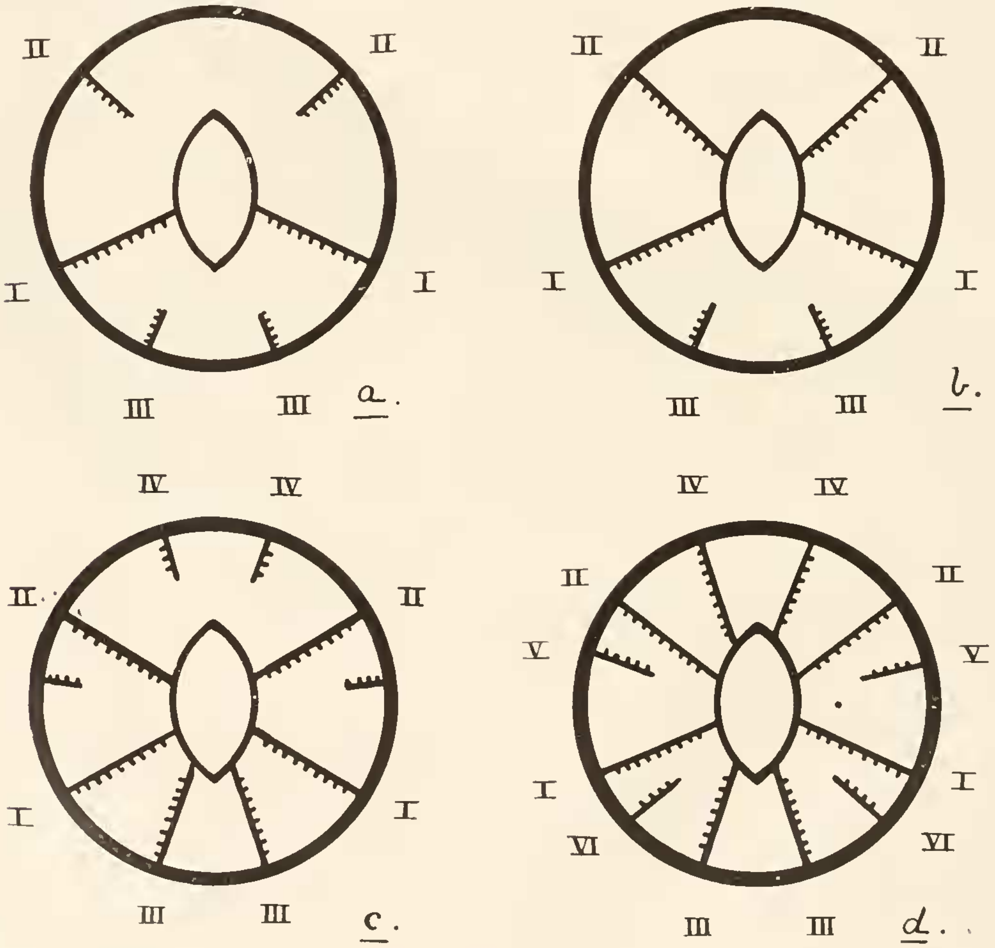

Fig. 15 (*a–d*).

Favia fragum.—Figs. 15. Diagrammatic figures illustrating the mesenterial sequence and fission in larvæ. *a*, Larva with three pairs of protocnemes, of which only one pair is complete (*cf.* Pl. XIV, fig. 112). *b*, Larva with three protocnemic pairs, of which two are complete (*cf.* Pl. XV, fig. 113). *c*, Larva with five pairs of protocnemes, of which three pairs are complete and two pairs incomplete (*cf.* Pl. XV, fig. 115). *d*, Larva at stage of fixation, with Edwardsian mesenteries complete and fifth and sixth pairs incomplete.

New polyps are added to the colony by division of the older polyps, apparently never by budding. A polyp sometimes exhibits two or three oral apertures on a single elongated or triangular disk, surrounded by a single system of tentacles; and in the different polyps of any colony all stages can be traced in the separation of the results of fission. It is therefore a very favorable species for the study of polypal fission. G. von Koch (1890) has already described the process as it occurs in the corallum of the nearly allied species, *Favia cavernosa*.

Fortunately, also, in *F. fragum* a complete series of stages illustrating the development of the mesenteries within the larva and young polyp is available, a series extending from the larva with only one pair of complete mesenteries to polyps with such a number as results in fission. The oldest stage reached by the mesenteries of the simple polyp is represented in fig. 15*g*, but the earlier stages may be briefly noted (figs. 15 (*a–f*)).

The twelve primary mesenteries are all developed at or shortly after the time of settling, when the larva exhibits the conditions represented in fig. 15*d*, four pairs of mesenteries complete and two pairs incomplete. Free swimming larvæ, extruded from mature polyps, are readily obtained, but can with difficulty be induced to settle, and development proceeds very slowly. However, on foreign objects, such as dead coral or old shells, to which the mature colonies are adherent, young polyps are sometimes found in different stages of development. These have grown from larvæ which on extrusion settled around the parent, and it was from such larval polyps that the stages represented in the text figures were taken.

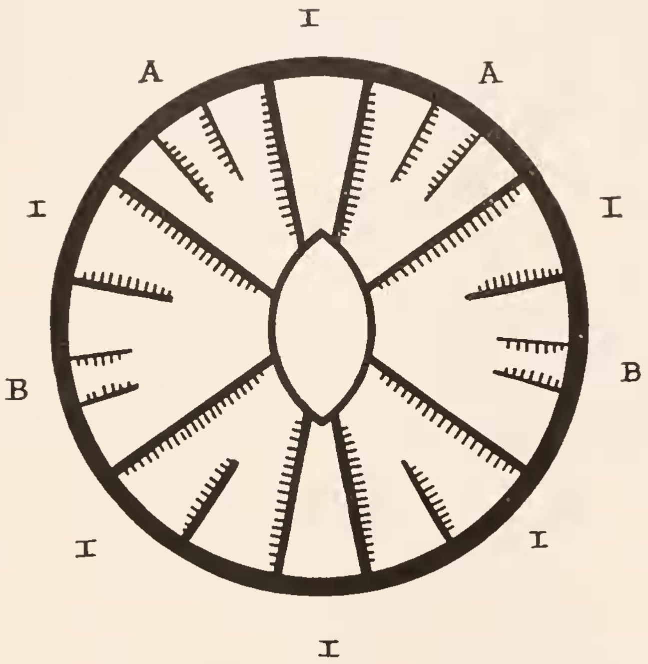

Fig. 15*c*.

Favia fragum.—Young polyp with four pairs of metacnemes (A, A; B, B). The succession of the second-cycle mesenteries is bilateral, from the dorsal to the ventral aspect (*cf.* Pl. xiv, fig. 109.)

Fig. 15*e* is from a young polyp in which four isocnemic pairs of mesenteries are present, in addition to the primary twelve. In the upper stomodæal region all the latter are inserted on the stomodæal wall, but the fifth and sixth pairs become free before the termination of the stomodæum is reached, and at this place the protocnemes are in exactly the same condition as in fig. 15*d*. The four pairs of new mesenteries are situated within the dorsal and middle primary exocœles on both sides of the polyp, and the dorsal pairs are somewhat further developed than the middle pairs.

Fig. 15*f* represents the mesenterial condition obtained from a transverse section through the lower part of the stomodæum of another decalcified polyp. The six protocnemic pairs are now all complete, and six alternating pairs of metacnemes are fully established as a second cycle. The next figure, from a somewhat larger polyp, shows the commencement of the third cycle of mesenteries (fig. 15*g*); its development also is proceeding by isocnemic pairs in a dorso-ventral or antero-posterior order.

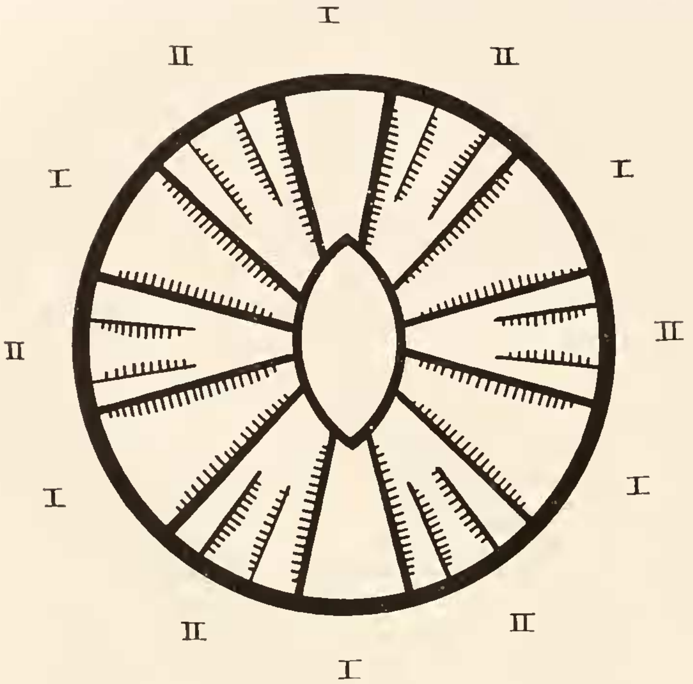

FIG. 15*f*.

Favia fragum.—Young polyp in which all the pairs of protocnemes (I) are united with the stomodæum, and the six pairs of first-cycle metacnemes (II) are developed.

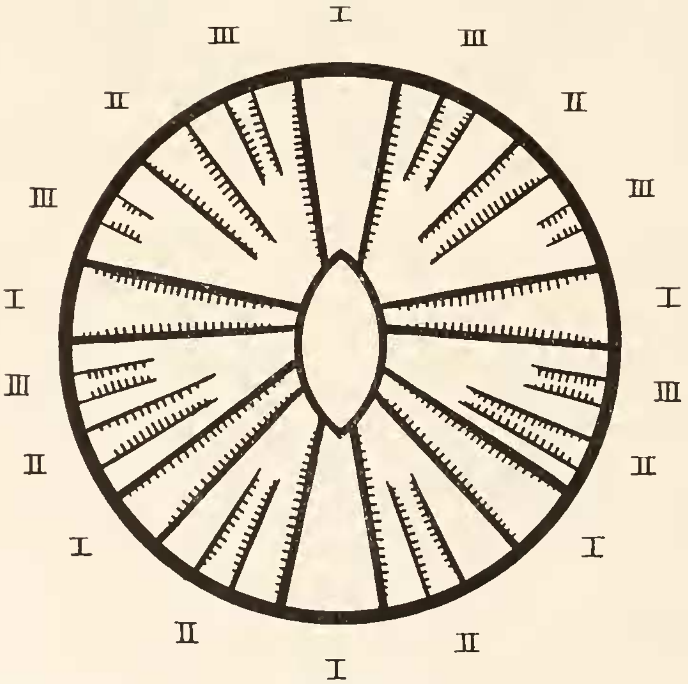

FIG. 15*g*.

Favia fragum.—Polyp with six pairs of second-cycle metacnemes (III). The succession is from the dorsal to the ventral aspect.

The polyps of *Favia* growing directly from larvæ are thus seen to follow a very definite sequence in their mesenterial growth, a sequence which bears the closest resemblance to that characteristic of other larval corals which have been examined. Each is provided with two pairs of directives, and the mesenteries are arranged in two or three radial cycles, according to the usual hexameral plan. It is at about the stage represented by fig. 15*g* that fission is introduced.

Two larval polyps were secured, each provided with two oral apertures, but still surrounded by only one system of tentacles and a simple column wall. They thus represent the earliest stage in fission. At such a stage the polyps are very short, and rather irregular in form when preserved, so that it is practically impossible to secure in one section the complete arrangement of the mesenteries around the stomodæum. The diagrammatic figures are therefore constructed by combining the relationships of the mesenteries in the various serial sections. In each polyp the stomodæum has been divided throughout its length into two distinct tubes, and a definite number of mesenteries is associated with each.

The mesenterial system of one of the double polyps is represented by fig. 16*h*. Compared with the stage in fig. 15*g* two additional pairs of mesenteries have become complete, so that four pairs are inserted on each stomodæum. Instead of the two new complete pairs arising as a pair on each side of the directive plane, as considerations of symmetry would suggest, both are situated on one side of the angulated directive axis of the polyp, though from the section alone it is impossible to say which of the four pairs actually represent the additions. The members of the second cycle include only a single pair of mesenteries in each exocœle, except in the two exocœles adjacent to the right pair of directives, where third-cycle pairs are developed.

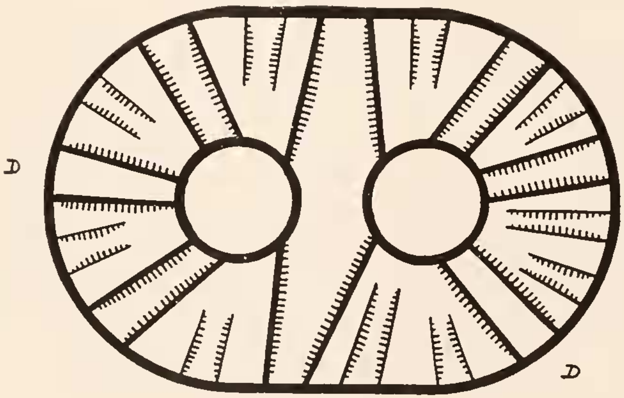

Fig. 16*h*.

Favia fragum.—First stage of fission in a larval polyp.

The two polypal halves are thus nearly alike, the original single stomodæum having been divided practically down its middle, so that half the mesenteries are attached to each moiety. The plane of fission crosses the directive axis, passing through the entocœle of two lateral pairs of complete mesenteries on opposite sides. Growth is taking place more rapidly at the upper right side than elsewhere, and the pair of directives has thus been pushed to one side of the median plane, so that the directive plane no longer divides the polyps into equal halves.

Were the halves to be completely separated at this stage, it is clear that a pair of mesenteries would be formed in each new polyp, by the approximation of a mesentery from the two opposite sides, the musculature in the two moieties being on the faces turned toward each other; an ordinary pair of mesenteries would be thus produced, and each polyp would have but one pair of directives. Thus, from the beginning, an important difference in the nature of the mesenteries would be established between fission polyps and single polyps reared directly from larvæ; the distinction between the orders to which the mesenteries primarily belonged also begins to be lost.

Fig. 16f represents the mesenterial plan in the second bioral polyp. In the living condition one oral aperture was much smaller than the other, appearing as a mere perforation in the disk, and sections reveal that a less number of complete mesenteries are associated with it than with the larger. In the diagram the smaller stomodæum is to the left, but is represented equal with the other. In the actual transverse sections it displays eight strongly marked vertical ridges, corresponding with the eight mesenteries attached to its inner side, while the large stomodæum bears ten. Here, again, it is seen that the plane of fission passes through the entocœle of two opposite pairs of lateral mesenteries, and growth is proceeding more rapidly at one region—to the lower right—of the polyp than at another, so that the directive axis does not coincide with the longer diameter, but is turned toward the dorsal surface.

Attention may now be directed to the fully developed polyps constituting a colony of *Favia*, in order to ascertain what are the results of fission upon these. As already remarked, the mature polyps are found to exhibit very varied conditions with regard to the stage of fission. They are rarely circular in contour, but polygonal or greatly elongated, and at times deeply angular; in the majority of adult polyps only one oral aperture is surrounded by a tentacular system, but sometimes two or three mouths occur on a single disk.

A transverse section of a decalcified polyp is represented on Pl. XIII, fig. 93, and indicates much variability and irregularity in the disposition of the mesenteries, differing greatly from the perfect regularity of the early larval polyps. The organs are paired throughout, but no regular hexameral cyclic arrangement can be established. Different stages of growth are represented in different regions; in some places there is an indication of a tricyclic plan, but more often only a dicyclic arrangement is manifest, and at times this is obscured by three or four pairs of mesenteries of equal ordinal value occurring together.

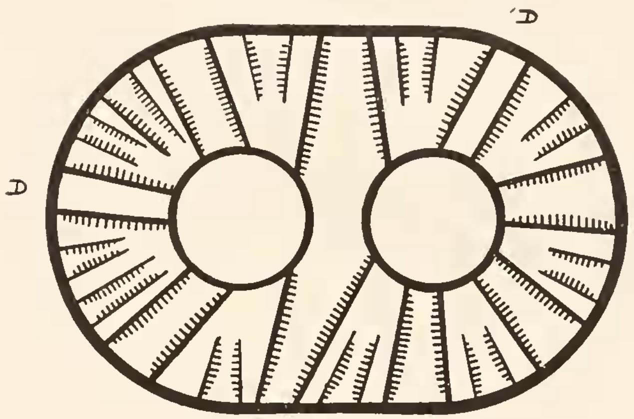

Fig. 16f.
Favia fragum.—First stage of fission in another larval polyp.

In the upper part of the stomodæum all the mesenteries may be complete, except a pair here and there in process of growth, but in passing downward some pairs become free in advance of others, indicating that they are not all of the same ordinal value.

The mesenterial pairs are always isocnemic, and the retractor muscles are invariably on the faces turned toward one another; in transverse sections of over a dozen polyps examined no directives occurred.

Adult polyps of the genera *Isophyllia* (p. 449), *Agaricia* (fig. 161), *Mæandrina* (fig. 141), *Colpophyllia*, and *Dichocœnia* (fig. 119) display a like irregularity of mesenterial arrangement and absence of directives. The actual stages in fission have not been traced in these, but from their prevailing mesenterial arrangement it is manifest that the process proceeds in the same way as in the young polyps of *Manicina* and *Favia*.

Several Actiniæ also exhibit the phenomenon of fissiparity, and certain investigations have been made as to its influence upon the mesenteries and other organs. Dr. G. H. Parker (1899) has given an account of the longitudinal fission in the common Actinian, *Metridium marginatum* Milne Edwards, and shows that the asexually formed polyps do not reproduce all the features characteristic of the sexually produced individuals. In some of the specimens examined, Parker found that fission of the stomodæal tube was still incomplete, the organ being Y-shaped, a single inner end opening into the gastro-vascular cavity, and the two outer ends opening each through a distinct mouth on a single disk. Generally in the fission specimens each mouth was monoglyphic (provided with only one gonidial groove), instead of diglyphic, as in normal forms; and with the monoglyphic condition was associated only one pair of directives. No evidence was forthcoming as to the formation of new siphonoglyps or new directives in fission polyps, while there were practically twice as many non-directive mesenteries in double specimens as in single ones. In any given case the assumed plane of division passed through either two primary exocœles or two entocœles, never a primary entocœle on one side and a primary exocœle on the other. The production of regular hexamerous diglyphic specimens by non-sexual methods was not observed; such specimens were found to number about one-fifth of the total collected, and are with good reason assumed to be the products of sexual reproduction.

The West Indian stichodactylinous anemones, *Actinotryx sancti-Thomæ* Duch. and Mich., and *Ricordea florida* Duch. and Mich., also reproduce by discal fission, and frequently more than one oral aperture is present within a single tentacular zone. In the latter species as many as seven mouths have been found on a single disk, thus recalling such a coral form as *Manicina*. Professor McMurrich's (1889*a*) anatomical studies of these two species, and also mine (1900), have shown that the mesenteries in both species are irregularly arranged, and in some polyps no directives occur, while in others only one pair is present.

The results on polypal fission in corals may be thus summarized:

1. The larval polyps of fissiparous species develop for a time like other hexamerous species. Before the introduction of fission the mesenteries are regularly arranged in two or more alternating hexameral cycles, and two pairs of directives are present.

2. The first fission plane passes through the entocœle of two lateral mesenterial pairs, approximately at right angles to the directive plane and longer oral axis, and divides the stomodæum and the mesenteries attached to it into practically equal halves, so that only one pair of directives is inserted on each stomodæal tube.

3. For a time the products of simple fission continue their development according to the regular cyclic plan, but before long fission is repeated, and each stomodæum and the mesenteries associated with it may be again divided into equal halves, or one part may be larger than the other. In probably every division the fission plane is included within two opposite entocœles. At an early stage in the development of fission polyps growth may proceed more rapidly at one region than at another, and thus introduce irregularities in the cyclic plan.

4. Beyond the two primary pairs no new directive mesenteries are ever introduced, so that in any fissiparous colony, however large, only the protocnemic directives occur, situated widely apart, at what may be regarded as the two morphological extremities of the colony.

With such results before one, it is clear that care must be exercised in attempting to establish relationships from the absence of one or both pairs of directives in mature polyps of both corals and Actinians. The history of the individual polyp must be taken into account before such an occurrence can be regarded as a specific peculiarity. As a general rule, one would be justified in assuming asexual reproduction by fission for polyps with only one or no directives, especially if accompanied by irregularities in mesenterial growth.

FISSION IN PORITES.

Polyps displaying a bioral disk are very rare on colonies of *Porites*. After an examination of scores of living colonies of all the West Indian species, only a single example exhibiting this condition has been found, although polyps showing an increase of tentacles beyond the usual twelve are by no means scarce; from these all stages in the development of the mesenteries beyond the primary six pairs are readily secured. These proportions present a marked contrast with those of the closely allied polyps of *Madrepora*; enlarged polyps are frequently found on colonies of *Madrepora*, provided with two oral apertures, and twenty-four mesenteries are already present at one stage or another of their development.

For the most part, the enlarged polyps of *Porites* are circular in section, and any increase in the number of tentacles merely results in the enlargement of the polyp, without altering its outline. The polyp with two oral apertures had, however, assumed an oval form, but the tentacles remained disposed in a single cycle, as in ordinary polyps.

In a former paper (Johns Hopkins Circulars, June, 1900), and again on p. 446, it is shown that in *Porites* the increase of mesenteries beyond the protocnemic stage takes place axially, by the addition of bilateral pairs within either of the directive entocœles, and that in the end they constitute both isocnemic and anisocnemic pairs. In some polyps the new mesenteries are added within the dorsal entocœle, and in others within the ventral entocœle, but never within both chambers in the same polyp. All stages from the occurrence of a single pair of new mesenteries to six pairs have been already described.

Serial transverse sections of the *Porites* polyp displaying the bioral condition were prepared, and by studying these at different levels the arrangement of the mesenteries represented in fig. 17 has been established. Two stomodæal tubes are distinct throughout their length, and twelve pairs of mesenteries are present, six pairs associated with each stomodæum and arranged as in a single polyp. All the additional mesenteries have been added within the ventral entocœle, the inclosing directives (III, III) of which have been pushed widely apart. The figure should be compared with fig. 11c, on p. 470, representing the arrangement in a polyp also with twelve mesenterial pairs, but in which only one stomodæal tube occurs.

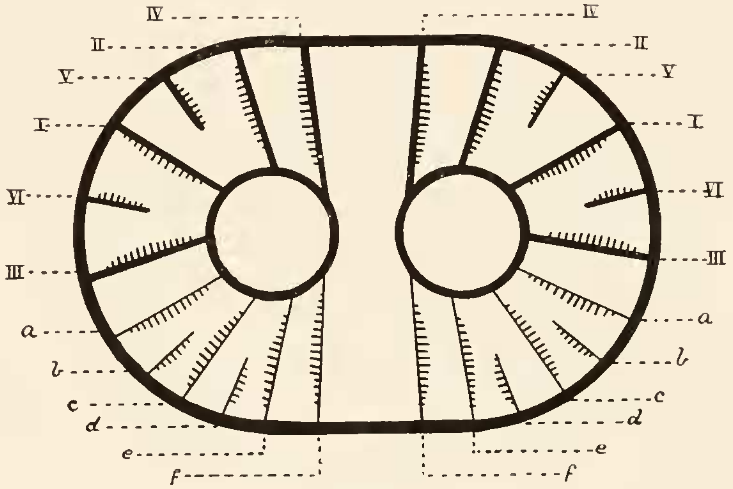

FIG. 17.

Porites.—Diagram illustrating polypal fission in a bud polyp. Within the entocœle of the ventral pair of directives (III, III) six bilateral pairs of mesenteries (*a-f*) have appeared, and the stomodæum has been divided into two distinct tubes. The complete and incomplete pairs of mesenteries and the musculature are so arranged that when the two polypal halves separate, each polyp will have six pairs of mesenteries arranged as in ordinary polyps.

From the figure itself (fig. 17), it would be difficult to determine within which of the two directive entocœles the increase has taken place, or which half is primary and which half secondary. In the actual sections the mesenteries on the ventral aspect are closer together, and disappear first in passing from above downward. From the sections of the various polyps at intermediate stages, it is clear that polypal fission in *Porites* is effected only after the successive addition of six bilateral pairs of mesenteries, the complete and incomplete members alternating in such a way that the moiety of the six new pairs on one side resembles the moiety of the six primary on the same side. When the two fission polyps are completely separated along the axial plane, a pair of directives will be formed for each polyp, by the approximation of one of the members of the primary dorsal directives (IV) and the corresponding member of the last-formed ventral pair (*f*).

The plane of fission coincides with the primary directive plane which passes through the primary dorsal and ventral directive entocœles and longer oral axis, and divides the enlarged polyp into equal halves with twelve mesenteries to each; of these, six are the protocnemes and six are new formations.

As the order of appearance of the mesenteries beyond the protocnemic stage in *Porites* differs from that in other coral polyps, so its method of fission is altogether different. In most corals the plane of fission is at right angles to the directive or median axis of the polyp, whereas in *Porites* it is along the directive plane; each of the two primary daughter polyps in ordinary fission has only one pair of directives, but in *Porites* the mesenteries are arranged exactly as in the larval polyp, and each fission polyp bears two pairs of directives. (See foot-note, p. 496.)

FISSION IN MADREPORA.

When describing, in a recent paper[a], the method of addition of new mesenteries in *Madrepora*, beyond the protocnemic stage, the process of fission was also noticed, so that for the present purpose it is only necessary to briefly reiterate the facts there brought forward. On examining most colonies of *Madrepora* with a lens, a few polyps are found which are slightly larger than the others, and bear more than the usual twelve tentacles, any even number from sixteen to twenty-four being represented. The tentacles form, however, only a single cycle, as in ordinary polyps (Pl. I, fig. 1 *l*.). Such polyps seem to occur anywhere over the surface of a colony, wherever vigorous growth is in progress, but have not been found in the oldest parts of colonies, nor on the under surface of palmate colonies, where conditions of growth are not very favorable.

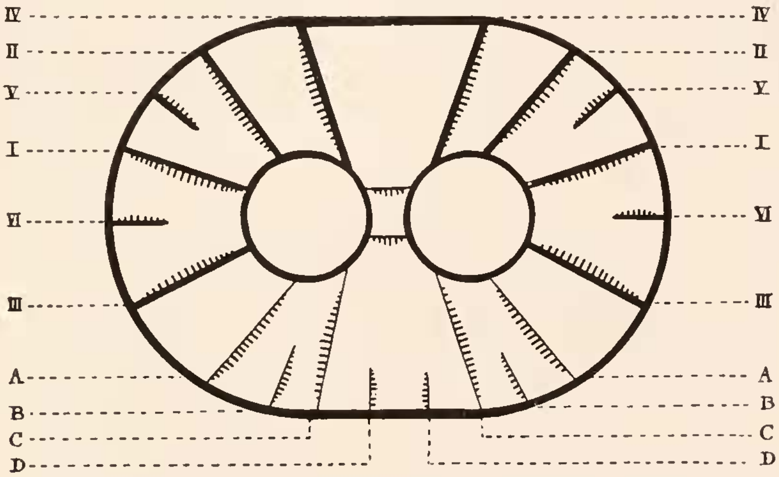

FIG. 18*a*.

Madrepora.—FIGS. 18. Series of diagrammatic figures illustrating polypal fission and the manner of increase of the mesenteries beyond the protocnemic stage. Two stomodæal tubes are present from the beginning, either connected by one or two mesenterial strands or altogether distinct. *a*, Four new bilateral pairs (A–D) are present within the ventral directive entocœle, and two others connect the two stomodæal tubes.

Most of the larger polyps are strongly oval, the longer axis being at right angles to the axial-abaxial plane. Out of forty or fifty enlarged polyps examined, only one or two did not already display two oral apertures, and of nearly thirty specimens sectionized transversely each bore two distinct stomodæal tubes. Compared with the enlarged polyps of *Porites* those of *Madrepora* are therefore characterized by the early production of the bioral condition.

Transverse sections reveal that in practically every case twenty-four mesenteries—that is, double the number in ordinary polyps—are already developed, though in different examples they exhibit somewhat different relationships. Sixteen complete mesenteries occur, and the remaining eight are incomplete, the paired arrangement agreeing with that of simple polyps.

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[a] “The Morphology of the Madreporaria.—II. Increase of Mesenteries in *Madrepora* beyond the Protocnemic Stage.” Ann. Mag. Nat. Hist., ser. 7, vol. x, 1902.

The different polyps studied exhibit one or another of three successive stages toward complete fission. These are diagrammatically represented in figs. 18 (*a–c*). The primary mesenteries are indicated by thicker lines, and are numbered from I to VI; the new mesenteries are denoted by the letters A to F, no successive order in their appearance being assumed thereby.

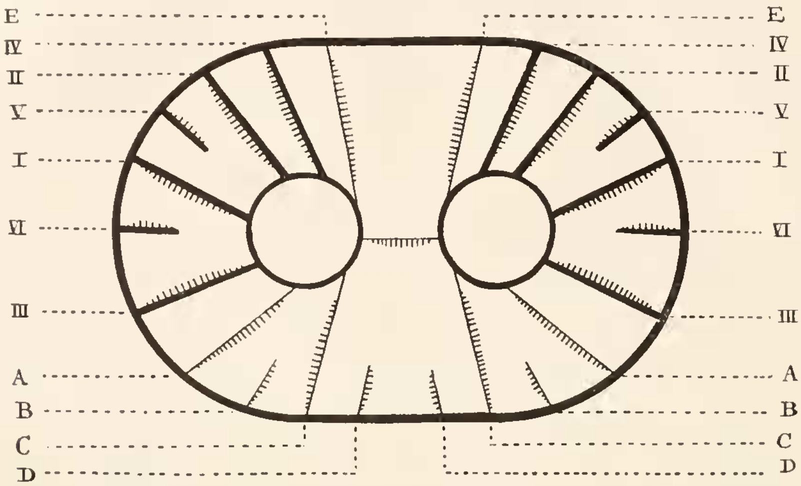

Fig. 18*b*.

Madrepora.—Fission continued. The same number of mesenteries are still present within the ventral directive entocœle, and a single pair (E, E) occurs within the dorsal directive entocœle, while only one mesenterial strand connects the stomodæa.

The figures reveal that new mesenteries are added in bilateral pairs, disposed axially in both the dorsal and ventral entocœles. No stage in which less than twenty-four mesenteries were present has been found.

Special interest attaches to the mesenteries in figs. 18*a*, 18*b*, which connect the two stomodæal tubes. In fig. 18*a* two of these are present, in fig. 18*b* only one, while in fig. 18*c* the connection has ceased altogether. In the paper already mentioned, it has been shown that these connecting mesenteries are a result of the practically simultaneous division of the primary stomodæum and the appearance of the new mesenteries. The adjacent mesenteries, situated between the two

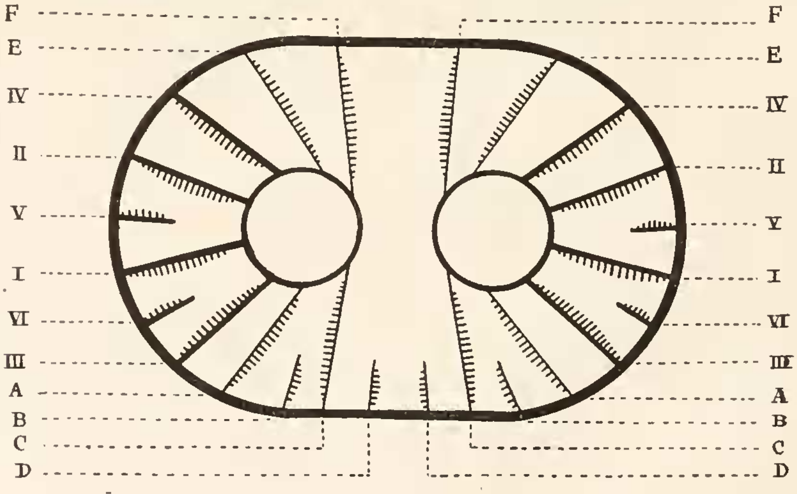

Fig. 18*c*.

Madrepora.—Fission continued. Two mesenterial pairs (E, F) now occur within the dorsal directive entocœle, and the stomodæal tubes are wholly disconnected. The macrocnemes and microcnemes and arrangement of the musculature on the faces are such that if the polyp were divided into two halves along the median axis the mesenterial arrangement in each polyp would be the same as in an ordinary polyp with only six pairs of mesenteries. (*cf.* Pl. I, fig. 4.)

stomodæal tubes, for a time retain this connection throughout the length of each stomodæum. Serial transverse sections indicate that later the middle portion of each connecting mesentery begins to grow radially across the disk, and that when it reaches the vertical column wall it divides into two distinct mesenteries, which constitute a bilateral pair. The division extends all the way from the upper to the lower termination of the stomodæal tubes, the successive stages in the process being easily followed. As shown by fig. 18*b*, the dorsal connecting mesentery becomes divided and stretches to the column wall in advance of the ventral member.

That no earlier stages, exhibiting a sequence in the appearance of the six pairs of new mesenteries, have been met with, such as are described for *Porites*, seems strongly to suggest that the additional six pairs arise practically simultaneously, in all probability *pari passu* with the division of the primary stomodæum. In the earliest bud polyp of *Madrepora* which has been obtained, representing a stage before any tentacles appear, all the twelve mesenteries are already present, and the oral perforation appears to have been just established (p. 497). It would also seem that in the formation of new polyps by fission a like simultaneous development takes place, and thus no intermediate stages between the twelve and twenty-four mesenteries are to be expected.

The results from the two methods of asexual reproduction in coral polyps—budding and fission—may be thus contrasted:

(1) Polyps arising as buds pass through the same stages as regards the order of appearance of the tentacles, mesenteries, and mesenterial filaments as the larval polyps of the same species, and the adults of both are alike.

(2) Excepting *Porites* and *Madrepora*, polyps originating by discal fission, whether completely or but partly separated, never wholly resemble the sexually-produced polyp. No new pairs of directives are formed, and the mesenteries do not assume a hexamerous or other regular cyclical arrangement.

(3) Polyps of *Porites* and *Madrepora* arising by fission resemble larval polyps in having two pairs of directives and four anisocnemic pairs of mesenteries. (See foot-note, p. 496.)

SEXUAL REPRODUCTION.

DISTRIBUTION OF GONADS.

Although the asexual method plays such a prominent part in coral growth, yet the production of sexual elements, for the formation of entirely new individuals, appears to be quite as important as in other groups of animals where sexual reproduction alone prevails. In West Indian waters, colonies of *Favia fragum*, *Manicina areolata*, *Siderastræa radians*, and *Porites clavaria* seem to be nearly always fertile, while species of *Madrepora*, *Orbicella*, and *Cladocora* are, as a rule, found without sexual cells.

Several observations upon the distribution of the gonads in the Madreporaria have been recorded by other writers, but, as in the Actiniaria, no general rule is apparent with regard to the monœcious or diœcious character of the polyps. Thus Moseley (1882) found *Seriatopora* to be unisexual; Fowler mentions the occurrence of ova only in *Madrepora durvillei*, *Turbinaria*, sp., and in *Sphenotrochus rubescens*, while *Pocillopora brevicornis* is monœcious. H. V. Wilson merely states that *Manicina areolata* is hermaphrodite. Gardiner (1900, p. 367) found all the polyps of *Cœnopsammia* which he examined to be female, without any trace of male generative cells.

In the course of the present studies many instances of fertile polyps have occurred. A portion of a colony of *Mæandrina labyrinthica* sectionized bore gonads on almost every mesentery, and in this case ova and spermaria were closely associated. In a few instances both kinds of sexual cells are found on the same mesentery (Pl. XX, fig. 140), but usually they are developed on separate mesenteries, the number of male mesenteries being greatly in excess of the female. The merest suggestion of an alternation of male and female mesenteries is manifest; thus, one member of a pair may bear spermaria and the other ova, but at other times two or three ova-bearing mesenteries are intercalated between a number of sperm-bearing mesenteries. Four to eight spermaria may be present on a single mesentery in section; but the number of ova is much less, usually one or two, rarely reaching four or five. In the hermaphrodite mesenteries the ova are invariably situated toward the fixed end of the mesentery, and the spermaria nearer the free edge, that is, more central.

Favia fragum is likewise monœcious, and in this species also the two kinds of sexual cells may occur on the same mesentery, though more often they are on different mesenteries within the one polyp. In one large colony examined, the cavity of practically every polyp was crowded with larvæ, all at the same stage of development. In addition to these the mesenteries were swollen with spermaria and ova, all apparently at a similar stage toward maturity—the ova having a large nucleus and nucleolus, and the spermaria with the tails of the spermatozoa already developed.

On a colony of *Porites clavaria* most of the individual polyps contained several free larvæ, again all at about the same stage of development. In this instance, ova only were present on the mesenteries, usually one large egg to each, and of numerous polyps examined from the same colony none bore male sexual elements. In transverse sections of a polyp of *Madrepora palmata* a single ovum occurred on three of the four lateral complete mesenteries, but not on any of the directive mesenteries.

Female gonads were moderately developed in a colony of *Isophyllia dipsacea*. In transverse sections some of the mesenteries exhibited three or four ova, restricted in their distribution toward the insertion of the mesentery in the body wall. Most of the mesenteries of a polyp of *Orbicella radiata* also contained ova, again situated toward their insertion in the polypal wall; likewise polyps of *Siderastræa siderea*. In the last the ova were greatly distorted and irregular in form, as if adapting themselves to the very narrow interseptal loculi.

From the above examples, it is impossible to say how far sexual differentiation has proceeded within Madreporarian polyps. In all instances where a unisexual character would be indicated, only female cells have been found, and then somewhat sparsely. Spermaria have never been found alone, but always in association with large numbers of ova.[a] It may be that coral species are mainly monœcious, but that ova are first developed (protogynous), and later spermaria, either on the same or different mesenteries. Further, the ova are, as a rule, restricted toward the fixed or peripheral margin of the mesentery, while in Actiniæ generally they are disposed about the middle of the radial length of the mesentery.

Apparently very little importance can be attached to the particular mesenteries on which gonads may occur, for where present in numbers they are found on practically all the mesenteries, both complete and incomplete. In *Orbicella radiata* any of the mesenteries of the three cycles may bear ova; as shown on Pl. IX, fig 68, ova occur on a small incomplete mesentery, while they are not developed on the larger complete member. In Actinian studies the distribution of the gonads on particular mesenteries is considered to be of some importance for systematic purposes, but manifestly the production of a few sexual cells on certain mesenteries can not be of much significance, when in riper polyps they may possibly be found on all the organs.

Within its lifetime a polyp may give rise to more than one series of ripe sexual cells, for individuals charged with fully developed larvæ also contain numbers of nearly ripe eggs, still within the mesoglœa of the mesentery.

Viviparity would appear to be the rule among corals, though Wilson records the extrusion of eggs and semen from *Manicina*, and I have also found this to happen in *Favia*. It may be doubted whether such occurrences take place under normal conditions, as in both instances highly developed larvæ have also been found within the gastric cavity. Similar promiscuous extrusions of sexual cells are likewise found to take place among anemones. From *Rhodactis sancti-Thomæ*, *Aulactinia stelloides*, and others unfertilized eggs and semen have been found to be extruded in abundance, while from both species mentioned larvæ at an advanced stage of development have also been obtained.

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[a] Miss Pratt (1900) describes *Neohelia* as probably monœcious, spermaria only being present.

From the few records yet available, it is impossible to determine how far the different species of corals have any regular breeding season; such would scarcely be expected under the uniform conditions of temperature characteristic of tropical waters. During the month of July four or five different colonies of *Siderastræa radians* were collected, all having polyps charged with free larvæ, while other collections made at different times from the same locality never yielded fertile colonies. From another locality larvæ of this species were secured during the middle of March.

Most of the larvæ to be here described were collected in the early months of the year (March, April); but larvæ of *Manicina areolata* and *Favia fragum* seem to be extruded nearly the whole year round.

SPERMARIA AND OVA.

In their detailed structure, the spermaria and ova of corals are much like the corresponding elements in the Actiniaria. A mesentery bearing two spermaria, in addition to three ova, is represented on Pl. XX, fig. 140, taken from *Mæandrina*. The fertile portion of the mesentery is greatly swollen, and the mesoglœa is thin and surrounds each ovum and spermarium as a very delicate sheath. The mesenterial epithelium has undergone certain modifications; toward their base the cells are much vacuolated, and without any recognizable protoplasmic contents. Cell limitations are not obvious, and the nuclei are arranged in a very definite zone toward the margin, along with the other protoplasmic contents of the cells.

The spermaria are crowded with deeply-staining, spheroidal, sperm cells, each with several still more deeply-staining particles or nuclei. A similar stage has been figured by Professor Hickson for *Alcyonium* (1895), and also described by Ashworth (1899) for *Xenia*. Occasionally a central cavity containing a coagulum is already developed, and here and there this is filled with the projecting tails of the spermatozoa. Without any doubt the ova and spermaria are developed from the mesenterial epithelium, as in other Anthozoa, and the cells wander into the mesoglœa and become encapsuled by it, but none of the earliest developmental stages have been found.

The spermaria from another colony of *Mæandrina*, instead of being nearly spherical, are narrow, and extend along the transverse length of the mesentery for some distance, and display constrictions, as if made up of four or five fused spermaria.

On one occasion, ripe spermatozoa were observed in the act of extrusion from a polyp of *Favia fragum*, the process taking place by the same jerking motion as when larvæ are liberated. They were of the same form as those of *Actinia equina*, described and figured by Lacaze-Duthiers, that is, a pear-shaped head with a laterally fixed tail.

A mesentery bearing two large ova is represented in fig. 146, again taken from *Mæandrina*. The eggs contain a large amount of vacuolated, finely granular yolk. The vacuolization is very uniform except peripherally, where the ovum stains more deeply, owing to the greater concentration of the protoplasm. In the same region deeply-staining granules are also numerous. The germinal vesicle is large and homogeneous in structure, and is unaffected by carmine stains, but readily takes up aniline blue. The germinal spot is usually situated close to the margin of the germinal vesicle, and differs from the latter in staining intensely in borax carmine.

White, spheroidal, unfertilized eggs were extruded singly from *Favia fragum* on several occasions, after floating around in the gastric cavity for several hours. Examined under the microscope, the ova underwent a great variety of irregular movements for about an hour, sending out lobate processes, first from one region and then rapidly from another.

The experiences of von Koch, Wilson, Haddon, and those here recorded render it manifest that the eggs in coral polyps are ripened in batches, not a few at a time, and that the larvæ develop equally; for in all cases where larvæ have been obtained from any polyp they occurred in numbers, and practically of the same age, while many far advanced eggs were present in the mesenteries preparing for another series. This is usually the case in the Actiniaria, but exceptions may occur, as where larvæ at all stages have been secured from the same polyp at one time. Fowler (1888, p. 13) states that the ova in *Sphenotrochus rubescens* were in various stages of maturation.

LARVÆ AND POSTLARVAL DEVELOPMENT.

In all corals yet observed, the segmentation of the ovum and early stages in the development of the larva take place within the internal cavity of the polyp, and are therefore not easily accessible for study. The extrusion of a few eggs and semen, which sometimes occurs, appears to be fortuitous in character, and is not to be regarded as the normal method of sexual reproduction. It is a little remarkable, that in the many sections of adult polyps which have been prepared, none of the intermediate stages between the egg and the fully developed larva have been secured, though fertile polyps, and others containing free advanced larvæ, are by no means rare.

Probably by keeping under observation, for a lengthened period, colonies which are known to be fertile, it would be possible to secure the earlier embryonic stages; polyps which are charged with advanced larvæ often contain in addition nearly ripe eggs, from which another batch of larvæ might soon be expected.

From the colonies of *Manicina areolata*, which H. V. Wilson had under observation for a period of several months, eggs, semen, and larvæ in very different stages were extruded. The first specimens of coral poured forth eggs and semen on the 15th and 17th of March, while on the 20th the polyps had given birth to larvæ a little more advanced than the planula. After this date only larvæ were ejected, their stage of development becoming much more advanced as the Bahama season progressed.

Among Actinians also the larvæ are usually ejected in an advanced stage of development; but unfertilized eggs and semen are extruded from a few forms—*Urticina crassicornis*, *Metridium marginatun*, *Sagartia parasitica*, and *Cerianthus membranaceus*, so that different investigators have found it possible to follow the segmentation and early embryonic stages of these.

Manicina areolata is the only coral in which the segmentation and formation of the germinal layers has hitherto been followed. But the early stages of development, as far as the formation of the skeleton, seem so completely alike in the Madreporaria and Actiniaria that the fuller details obtainable within the latter group may be considered to hold for the former. Appellöf (1900), in his admirable paper, "Studien über Actinien-Entwicklung," has followed very completely the early stages in the development of the Actinian *Urticina crassicornis*, and at the same time reviews the results of other workers throughout the Zoantharia in the light of his own.

The following account will be restricted to a description of the larvæ either upon extrusion or shortly after, and as far as their subsequent development has been traced. During the course of the present investigations numerous larvæ of the following species of corals have been obtained: *Manicina areolata*, *Favia fragum*, *Siderastræa radians*, *Porites clavaria*, *Isophyllia dipsacea*, and *Agaricia agaricites;* not always, however, under circumstances in which their future history could be followed. In some cases it has been possible to trace their growth through various stages, but in others only the larvæ themselves are available for study. Some of the larvæ were preserved directly in corrosive acetic, and others in formol. The former method gives the best results. During preservation mucus was often extruded from the unicellular ectodermal glands, resulting in the adherence of foreign particles to the larval wall; often also the larvæ collapsed when transferred to the preserving medium.

Where the superficial tissues of viviparous polyps are partly transparent, the larvæ can be seen moving about within the gastro-cœlomic cavity, coming into view above and then disappearing below. Very often they enter the tentacles, and may remain there for some time, so that when the polyps retract they give rise to small protuberances of the surface. Whether the motion within the polypal cavity is due to the larva's own ciliary activity, or is brought about as a result of the general circulation of the internal nutrient fluid, is not readily ascertained; certain larvæ are provided with cilia and able to swim about immediately on extrusion, while others remain motionless for a short time, showing that cilia are not yet active.

The actual extrusion of the larvæ seems always to take place suddenly, not with the slow convulsive movements more usual in parturition in other groups. In *Manicina areolata* the larvæ were ejected through the mouth in batches, a dozen or so at a time, by a peculiar jerking motion of the adult; but in *Porites clavaria*, *Favia fragum*, and *Siderastræa radians* they appeared singly, or only two or three at a time. Probably the larvæ are able to made their exit through the tips of the tentacles, as well as through the mouth, though owing to the rapidity with which the process takes place I have never been able to assure myself of this method, even when, as in the case of *Siderastræa*, colonies have been watched for hours. Von Koch states (1897) that the larvæ of *Caryophyllia cyathus* pass through the tips of the tentacles. The various polyps of a colony continue to give out larvæ for several days, or even for a week or two, and then the supply ceases, or for some time one or two individuals may appear at long intervals.

Development appears to proceed equally within most of the polyps in any colony. In the fertile colonies of *Favia* or *Siderastræa* the majority of the polyps contained larvæ all at the same stage, and in *Porites* such was the case with most of the polyps within any restricted area.

On first extrusion the larvæ of corals are spheroidal, oval, pear-shaped, or elongated rod-like bodies, varying from 1 to 3 mm. in length, the outer surface uniformly ciliated throughout. The various forms assumed by the different larvæ of *Favia fragum*, extruded about the same time, indicate the more usual shapes (Pl. XIII, figs. 96–100). Lacaze-Duthiers (1873) figures the larva of *Astroides calycularis* as elongated and assuming a spiral form, von Koch (1897) that of *Caryophyllia cyathus* as pear-shaped. The individual larva, however, often manifests the power of retraction and of altering its shape, so as to be at different times oval, pear-shaped, spheroidal, or flattened and cake-like. In the majority of cases, one end, usually the anterior during progression, is much broader than the other, though when the larva has been extruded for some time these relations are frequently reversed. Thus, the pear-shaped larva of *Favia fragum* has at first the broad end at the aboral forward pole, but later the broad end is oral or posterior and the narrow end is aboral. A similar alteration of form has been noticed in *Siderastræa radians*, but most of the larvæ of this species have a narrow aboral and a swollen oral pole from the beginning. Twin larvæ, with two oral extremities and one aboral, have been extruded by polyps of the species just mentioned. No coral larva has yet been described in which the aboral extremity bears the tuft of larger, less mobile cilia sometimes met with in Actinians.

Coral larvæ are able to swim about either immediately on extrusion or shortly after. For the first few minutes they may remain motionless, either at the surface of the water or on the bottom of the vessel, then, cilia having been formed, active movements of both rotation and translation commence. Some gyrate throughout the depth of the water, coming to rest from time to time; others remain nearer the surface or accumulate around the sides of the vessel. Within one to three days a few of the more vigorous examples would become attached to the sides of the glass vessel or other object, and remain thus for some time, then become active again, and afterwards refix themselves. But the great majority seemed unable ever to settle, and continued alive for days or weeks, without much motion, and apparently without undergoing further development. If fixation did not take place during the first two or three days it was never found to occur after, though some of Wilson's larvæ of *Manicina* settled after swimming around for three weeks.

When first extruded, coral larvæ are dense and opaque, and either colorless or slightly brown; afterwards they may become slightly distended, and as a result the wall appears thinner and more nearly transparent. Occasionally the larvæ are set free in a distended form, when they are more transparent from the beginning. The alteration from the opaque to the more transparent condition is brought about by an important change in the internal endodermal tissue, described below. Under the microscope the colorless or nearly colorless outer ectoderm can be distinguished from the inner endoderm, and in all species examined the latter bears zooxanthellæ, which give a yellowish color to the internal mass.

The oral pole, whether narrow or broad, is usually darkly colored externally. Examination of the living larvæ under the microscope, and also by means of sections afterwards, reveals that the color is due to the presence of numerous zooxanthellæ or yellow cells toward the oral end. Usually these occur within the ectoderm cells, but sometimes, as in *Isophyllia dipsacea* (Pl. XXV, fig. 165), they crowd the endoderm cells around the oral extremity, and the ectoderm contains comparatively few. In both cases the zooxanthellæ are densely aggregated toward the apex, which in consequence is the darkest area. In general the algæ are sparingly distributed throughout the endoderm, and thus give rise to the faint brown color of the larvæ as a whole. Only rarely do they occur beyond the oral region of the ectoderm.

From time to time the zooxanthellæ are seen to be set free from the ectoderm cells, and in the end they wholly disappear from the outer layer, the larva becoming uniformly colored. Occasionally they persist for a short time within the perioral area after the larva has become fixed.

The presence of numerous symbiotic zooxanthellæ within such a restricted region of the larva during its interpolypal existence, and their disappearance shortly after the larva is set free, are phenomena upon which no explanation has yet been offered. In no adult corals are zooxanthellæ found within the ectodermal cells; it is wholly a larval condition.

When the larvæ are first extruded, the oral aperture is usually indeterminable, but a very minute opening appears shortly after, often situated a little to one side of the actual apex, and later the wall immediately around the mouth becomes slightly depressed. Extrusions of zooxanthellæ, and what seem to be yolk granules in a mucus-like mass, have been observed to take place from time to time through the newly formed mouth. This phenomenon commences shortly after the larvæ are set free, and continues for some time. Lacaze-Duthiers (1873) has figured the ejection of waste material actually taking place in the larvæ of *Astroides*, and it is also found to be a common occurrence in Actinian larvæ. It is manifest that this is the larva's method of getting rid of the surplus zooxanthellæ, yolk, and cell débris remaining after the formation of the narrow endodermal layer from the original nearly solid internal tissue. Sections of late larvæ are generally found to contain free zooxanthellæ, and what seem to be cells in process of disintegration (fig. 112), while in early larvæ the interior may be wholly filled with a compact vacuolated tissue (Pl. XXV).

Some time after their extrusion, the larvæ may enlarge a little, and begin to lose their opacity, or this may not take place until they settle. Through the more transparent walls the internal attachment of the mesenteries can be seen, and their number and course determined. Usually three or four pairs of mesenteries are indicated at this stage, one or both of the lateral pairs generally extending as dark, thickened bands farther down the polyp than the two axial pairs (Pl. XVII, fig. 125).

In nearly all cases sections of the freshly extruded larva reveal an almost solid interior, into which the very narrow stomodæum has pushed, as it were, its way; also three or four pairs of mesenteries are more or less developed (Pls. XVIII, XXV). Afterwards the four pairs of mesenteries seem to grow quickly, so that by the time of settling all may be united with the stomodæum, two additional pairs—the fifth and sixth developmental pairs—having appeared in the meantime; the latter, however, never unite with the stomodæum for a long time after fixation. All the six pairs of protocnemes were already present in freshly extruded larvæ of *Isophyllia dipsacea*. Tentacular protuberances seem never to make their appearance before the fixation of the larva, nor has any trace of skeletal matter been observed during the free swimming stage.

Within a day or two after extrusion the individual larvæ settle by the forward aboral pole, on any suitable surface which presents itself, and usually independently of one another. Should the aboral extremity of the larva be narrow, it rapidly flattens after fixation; the larva as a whole shortens greatly, swells laterally, and for the first time the differentiation into basal disk and column is established.

Fixation may take place in close proximity to the parent colony, and in such cases probably directly after liberation. It is a common occurrence to find a few young polyps adhering to the lower, dead surface of colonies of *Manicina* and *Favia*. Lacaze-Duthiers (1899) has also shown that in the *Caryophyllia* obtained from Port Vendres "bouquets" of the coral have been produced, evidently by the larvæ fixing themselves on the exposed region of other corallites, and, thus attached, growing to their full dimensions and giving a semblance of budding or fissiparity to the usually simple coralla. Von Koch (1890) also describes "aggregated" colonies in *Balanophyllia*, which could only have originated in the same manner.

A still more remarkable instance of colony formation, from the union of individuals originally free and distinct, occurred during the fixation of the larvæ of *Siderastræa radians*. The larvæ settled in groups in such close proximity that when expanded the polypal walls pressed against one another, and produced angulated outlines. In one instance a colony thus produced consisted of thirty-two primarily free larvæ, in another twelve larvæ associated themselves, in a third seven, while several groups of three or four polyps were formed. Some of these colonies lived in small aquaria for three or four months, during which time the tentacles and skeleton appeared. To all appearances they would, under natural conditions, have given rise to actual colonies, indistinguishable from ordinary colonies produced by gemmation. (See foot-note, p. 495.)

Of the numerous larvæ extruded by corals comparatively few seem to settle, and in aquaria the greatest difficulty and uncertainty are experienced in securing permanently fixed individuals. Sometimes a number will become fixed, while under what appear to be exactly similar circumstances fixation seems impossible. In addition to the somewhat unnatural conditions under which the larva may be placed in aquaria, it seems not improbable that the ripeness of the larvæ for settling may also be a factor. In my experience, if fixation be not effected within two or three days after extrusion, it does not take place afterwards. The larvæ will then remain resting or slowly swimming about for an indefinite time, apparently undergoing no development whatever. Larvæ of *S. radians* have been kept thus for a period of twenty days.

Different measures were employed to provide the larvæ with suitable surfaces for fixation, and at the same time permit of their examination later. Glass dishes and small pebbles were placed in the vessels, and cover glasses floated vertically by means of pieces of cork. These provisions, however, were of little service. The most favorable position appeared to be the sides and bottom of the glass vessels in which the colonies were living. The larvæ being properly settled, the vessel was broken with care, and the fragments bearing the larvæ distributed to other vessels in which coral colonies were already established. Many larvæ were secured in this way, fixed to transparent pieces of glass, and could be taken out at any time, and examined in small glass dishes as transparent objects under the microscope.

Once the larvæ were fixed, they appeared quite vigorous and hardy, and continued their growth even under unfavorable conditions; while larvæ which remained unfixed, though kept alive and active for several weeks, never increased in size or underwent development in any way.

Ectoderm.—The larval ectoderm is very broad compared with the same layer in the adult polyp. In section the ectoderm of the larva of *Agaricia* measures 0.1 mm., and that of *Favia fragum* 0.08 mm. Most of the usual Anthozoan cellular elements are already differentiated at or before extrusion; gland cells, nematoblasts, supporting cells, and nervous elements occur, but no muscular fibrils have been recognized. No observations have been made on fresh macerated material, but the various cells separated somewhat freely from certain of the specimens preserved in formalin.

Both transverse and vertical sections of the ectoderm exhibit certain zones characterized by differentiations in the cellular constituents (fig. 165). The greater number of the nuclei are aggregated about the middle of the layer, and inwardly they occur in diminished numbers as far as the mesoglœa. By reason of the deeply-staining character of the nuclei their zone of distribution stands out strongly in moderately thick sections, and macerations show that it comprises the nuclei belonging to the supporting cells; the more deeply situated nuclei are those of the gland cells, developing nematocysts, and nervous elements.

The outer half of the ectoderm comprises the swollen portion of the gland cells and the mature nematocysts, embedded, as it were, in a matrix of supporting cells; the margin frequently shows the swollen bases of the cilia, which stain very strongly in methyl blue.

The inner zone is not well defined, and in early larvæ is usually characterized by the presence of large numbers of developing nematoblasts. These stain deeply, appear nearly homogeneous, but with a nucleus to one side, and are arranged irregularly at all angles to the other constituents; as they mature they migrate peripherally, and become arranged at right angles to the surface of the layer.

The gland cells are a very important constituent of the larval ectoderm, and their contents are nearly always finely granular, and usually remain unstained. Sometimes the vacuolar part extends nearly, if not altogether, across the layer, and on preservation the larvæ often throw out large quantities of mucus, when the cells become clear.

As already mentioned in describing the external characters, the ectoderm cells may contain zooxanthellæ, mainly restricted to the oral pole, but at times occurring sparsely throughout.

At the aboral extremity of all the larvæ examined the ectoderm undergoes an important alteration; nervous elements become developed to such a degree as to suggest that the region represents a special sensory organ. The general features of the differentiation are much the same in each species (Pl. XXV, fig. 165). From the narrow mesoglœa a number of delicate fibrils extend parallel with one another and at right angles to the layer, and unite in a reticulum which in sections seems largely made up of the cut ends of nerve fibrils. The nerve layer may be very broad, and on the outer side is continued into the ectoderm cells. The latter are usually more elongated, and more compactly arranged; the mucous cells are greatly diminished in numbers, and the nematocysts and supporting cells have undergone a corresponding increase.

The special nervous development is not restricted to the actual aboral pole, but extends some distance up the wall, gradually becoming weaker and weaker, until ultimately, a little below the middle of the larva, it is scarcely distinguishable.

I have described the occurrence of a similar sense organ at the aboral pole of the larva of *Lebrunia coralligens* (1899), and Professor McMurrich (1891) has found the same in the larva of *Rhodactis sancti-Thomæ*. It is suggested that the organ is in some way associated with the forward position of this end of the larva in swimming, and disappears when the larva settles by this extremity. Appellöf (1900) has found a less marked ectodermal modification at the aboral pole of the larva of *Actinia equina*, but in this species no special nerve layer is developed. The layer is clearer than elsewhere, and the cells are long and extraordinarily fine, and some even seem to terminate in two or more fine fibrils, while on the outside a group of longer, less mobile cilia occurs. Appellöf observed no corresponding differentiation in the aboral ectoderm of *Urticina*.

Mouth and Stomodæum.—When the larvæ are first extruded an oral aperture as a rule is indeterminable, though a few hours afterwards a small circular opening can be made out, and later the wall around may be partly depressed. Transverse and longitudinal sections through the oral pole of freshly extruded individuals also indicate that for a time the mouth and stomodæum are not functionally active, and the ectoderm at the entrance to the interior often appears without any break. In sections through the stomodæal tube an extremely narrow lumen occurs, but the condition of the canal does not suggest that ciliary activity has been established, any more than the nearly solid interior of many of the larvæ would permit of the circulation of a nutrient fluid. The stomodæal ciliation is not always distinguishable, yet when fully active the cilia here are the strongest in the whole polyp. The deeper parts of the ectodermal epithelium at this stage contain the developing stages of many nematocysts, and the nuclear zone so characteristic of the stomodæal ectoderm in adult polyps is not yet strongly differentiated.

The ectoderm never stops short all the way round at the actual inner termination of the stomodæal tube, but is partly reflected along the endodermal surface, and thence becomes continuous with the mesenterial filaments, passing down the free edge of whatever mesenteries are wholly complete (Pl. XVIII, fig. 127). In endeavoring to establish the homology of the mesenterial filaments, much significance has been attached to this reflected ectoderm, and to the apparent passage of the stomodæal ectoderm on to the mesenteries (p. 477).

Endoderm.—Much variation exists as to the condition of the interior of the larvæ when the latter are newly hatched. In some instances it is filled with a highly vacuolated tissue, so that the larva is a nearly solid mass of spheroidal cells; other larvæ are hollow toward the middle, but provided with a broad endodermal lining. A comparison of the figures on Pls. XV and XXV will give an idea of the different internal conditions which have been encountered.

The vacuolated tissue filling the cœlenteric cavity appears as if made up of distinct spheroidal or polygonal cells, each with a definite boundary, and having a nucleus applied to the wall. Each cell is occupied almost completely by a large vacuole, but around the walls are granules of different sizes which do not stain. The appearance of the tissue is the same throughout, in whatever direction the sections may be made. Zooxanthellæ are numerous and may be uniformly distributed, or, as in *Agaricia*, are more restricted toward the oral extremity and periphery (fig. 165).

In larvæ of *Agaricia* and *Isophyllia* the endodermal tissue is in its most compact condition, and in both transverse and longitudinal sections slits or lines of demarcation are present, which limit one portion of the tissue from another. Along the margin of the slits the cells have more contents, and the boundaries of the mesenterial filaments and more central part of the mesenteries are also shown, the tissue appearing as a matrix in which these organs are embedded. The slits thus serve to delimit a parietal, mesenterial, stomodæal, and middle endodermal tissue (Pl. XVIII). In some larvæ the slits are represented by wider, more definite spaces, especially in the stomodæal region, while below the stomodæum the middle endodermal tissue can be seen in process of breaking down. Only the middle tissue, however, undergoes disorganization; that lining the wall and mesenteries persists as a thickened mass for a long time. Where the process has continued for some time the middle of the larval cavity is occupied by organic débris, comprising granules of various kinds, fragments of cell walls, and zooxanthellæ (Pl. XIV, fig. 112). This is afterwards extruded by the larvæ shortly after the establishment of the oral aperture (Pl. XIII, fig. 96).

For a long time the parietal and mesenterial endoderm remains enormously thickened, arranged in high vertical ridges, all the cells of the same vacuolated character, in both respects differing from the epithelium of the mature polyps. G. von Koch (1897), in his paper on the development of *Caryophyllia cyathus*, and later in "Das Skelett der Steinkorallen," has drawn particular attention to the parietal thickenings of the endoderm in larvæ of this and a somewhat later stage. As a rule the endodermal thickenings assume a definite form and relation with the mesenteries, which varies as the latter increase in number. In the section of the larva of *F. fragum*, represented in fig. 116, they are ten in number, two axial thickenings and four bilateral pairs; at a later stage another pair will be formed, and ultimately a thickening will occur in each of the twelve mesenterial interspaces. Von Koch (1896) has found similar endodermal swellings in the corals *Astroides*, *Balanophyllia*, and *Caryophyllia*, and in the Hydroids *Coryne* and *Tubularia*; Haddon (1890) figures exactly similar structures in the larva of *Euphyllia*.

The thickenings correspond with the positions which later will be occupied by the calcareous septa, and von Koch has applied to them the term *Prosepta* (Vorsepten). It is not to be assumed that they in any way represent the septa, or are concerned in their formation, for they are just as well developed in Actinians, e. g., *Lebrunia*, which never form a skeleton. From their structure and arrangement, von Koch supposes that in the larva the endodermal thickenings function as elastic supporting organs; that they are the physiological predecessors of the septa. Morphologically they are seen to be the remnants of the vacuolated endoderm, which, at an earlier stage, practically filled the interior of the larva.

When the larva settles the thickenings still persist in the lower region, and extend intermesenterially along the base and for some distance up the column, as shown in the section of *Manicina* (fig. 137). The septal invaginations of the ectoderm arising later are formed within the prosepta, so that the skeletotrophic endoderm is greatly thickened from the beginning.

Apparently in the larval prosepta we have the precursors of the enormously thickened vacuolated skeletotrophic endoderm, already described as characteristic of the lower aboral region of a great number of corals.

The prosepta are thus the persistent representatives of the endodermal tissue, which at an earlier stage completely occupied the internal cavity of the larvæ. The middle portion of this tissue becomes disintegrated, and the débris extruded from the larvæ, while the peripheral portion persists, becomes associated with the skeletal ingrowths, and undergoes more or less histological alteration.

In the larva of the Actinian *Lebrunia* (1899) I have already described a somewhat similar, nearly solid condition of the interior, and in this case the tissue of the earliest larvæ showed definite narrow spaces, which were regarded as indicating a primitive cœlom. These spaces correspond with the narrow slits and limitations met with in the freshly extruded larvæ of

Agaricia and *Isophyllia*. In the later larvæ of *Lebrunia* the central part of the vacuolated tissue had become broken down, and cell débris and zooxanthellæ were seen to escape through the oral aperture; and thus the adult cœlenteron was produced, though for a long time the parietal and mesenterial endoderm remained greatly thickened.

Appellöf, toward the close of his paper, "Studien über Actinen-Entwicklung," discusses my conception that the endoderm of the larva of *Lebrunia* is for a time multilaminar, and concludes that I am mistaken in my interpretation of the appearances. He surmises that *Lebrunia* is exceptional in that its larval endoderm cells are greatly elongated and highly vacuolated, not that they represent a parenchymatous mass, as my observations imply. The various coral larvæ here investigated show that the more or less solid condition is by no means exceptional in the Zoantharia, but is rather the rule. The question at issue is whether the appearances presented by sections are due to the vacuolization of a comparatively few elongated cells, or whether the endodermal tissue at this stage is composed of numerous rounded or polygonal cells forming an embryonic parenchymatous mass.

In whatever direction sections are taken the appearances are the same, the tissue seeming constituted of rounded or polygonal elements; there is never a radiating appearance, such as would be expected did the cells represent a columnar epithelium. The absence of this can not be set down to the disappearance of cell limitations, for such are everywhere very obvious. Moreover, so far as can be judged, each vacuolated element is provided with a well-defined nucleus, adherent to the wall.

It is manifest, from all the stages available, that the central portion of the tissue becomes disorganized shortly after the larva's extrusion, when functional activity of the stomodæum has been established. As seen in sections, the middle of the larva at this stage is filled with granules of various kinds, some staining deeply and others colorless; zooxanthellæ and fragments of what seem to be cell walls are also plentiful. Were all the cells fixed to the mesoglœa by their base, we should then have to assume that their centripetal ends become disintegrated and the débris extruded, a proceeding which would hardly be expected to occur.

LARVA OF AGARICIA AGARICITES.

(Pl. XXV, figs. 165–167.)

A colony of *Agaricia*, freshly collected, extruded numbers of larvæ within a few hours, all of which were directly preserved. The specimens were opaque and about 3 mm. in length; some were strongly pear-shaped, and others nearly spherical, and all swam about from the beginning. So far as could be made out by examination of the living specimens under the microscope, no oral aperture was yet established; a few zooxanthellæ were present in the ectoderm around the oral extremity. Most of the larvæ partly collapsed on preservation, whether in formalin or corrosive acetic.

Sections reveal that the larvæ are all at the same stage of development. The interior is filled with a compact vacuolar tissue, leaving practically no free cavity, and six pairs of mesenteries are developed, all of which extend nearly the full length of the inner cavity; four pairs of the mesenteries are united with the stomodæum throughout its length, but the other two pairs nowhere reach it. Mesenterial filaments are already borne by all the six pairs of mesenteries, and become strongly developed toward the aboral extremity of the larva. Both transverse and longitudinal sections indicate that the oral aperture is not yet formed, though evidently just about to be so; the stomodæal tube already shows a definite lumen, but at its outer extremity the ectoderm cells still close over it, and would prevent any communication between the interior and the exterior. No ciliation of the stomodæal ectoderm can be made out, though this character is always very manifest in well-preserved examples of the adult polyps. That the cilia in this instance have not disappeared, owing to imperfect preservation, may be inferred from the fact that the external ciliation of the ectoderm is still clearly shown.

The outer ectoderm of the larva is a very broad layer, and the usual histological elements of the adult are already present, comprising supporting cells, gland cells, and nematocysts, with the addition toward the aboral extremity of a well-developed nerve layer. Zooxanthellæ are very limited in number and distribution. Only a few occur around the position at which the oral aperture will be formed, as noticed among the external characters. The cellular constituents of the ectoderm are distinctly shown in larvæ doubly stained with borax carmine and methyl blue, and the enlarged bases of the cilia are clearly distinguishable. Apparently on preservation none of the gland cells extruded their contents, and these are now stained with the carmine, while the supporting cells and nematocysts are stained blue. Most of the gland cells have finely granular contents, but others are clear, and they may extend nearly the whole width of the layer. The nematocysts are small and not very numerous. In the deeper parts of the layer are numerous clear, elongated bodies, staining blue, with the nucleus red, which in all probability represent developing nematocysts. The nuclear zone is very sharply limited on its outer margin, and the peripheral zone, wholly devoid of nuclei, occupies nearly one-half the thickness of the whole ectodermal layer, made up for the most part of the swollen gland cells.

About midway down the column wall an ectodermal nerve layer begins to appear. At first very feeble, it becomes better developed as the aboral extremity is approached, until at the actual pole it is very prominent. What seem to be delicate nerve fibrils extend vertically from the mesoglœa, and then unite in a broad meshwork; under high magnification the mesh exhibits the cut ends of very delicate fibrils, especially well seen in transverse sections. At the actual extremity the gland cells are less plentiful and nematocysts are more numerous.

Throughout the larva the mesoglœa scarcely attains any appreciable thickness, but appears as a mere dividing lamella between the ectoderm and endoderm; even in the mesenteries it is barely seen as a definite layer. Associated with its endodermal surface are nuclear bodies which stain deeply in methyl blue, and exhibit somewhat of a punctate character, as if nuclei in some mitotic phase, but, owing to their minuteness, no further details can be made out. Similar appearances occur also in connection with the mesoglœa of the mesenteries, and may perhaps be concerned in the formation of the middle layer.

The endodermal cells are spheroidal or polygonal, and almost completely vacuolated. Zooxanthellæ crowd the endoderm cells toward the oral end of the larva, and are sparsely distributed throughout; they show a slight tendency toward a restriction around the periphery of the endoderm. Although compact, the endodermal tissue presents a definite series of internal boundaries associated with the mesenteries, which indicate the lines along which cavities or passages will be formed when the larva becomes distended and the cœlenteric cavity is ultimately established.

The freshly extruded larvæ of *Agaricia* are somewhat exceptional in the degree to which the mesenterial development has already proceeded. In all the specimens examined the Edwardsian mesenteries are complete, and though the fifth and sixth pairs are yet free from the stomodæum they extend vertically nearly the whole length of the larva. The dorsal directives cease aborally a little in advance of the remaining three pairs of complete mesenteries.

Mesenterial filaments are strongly developed on the Edwardsian mesenteries, and less so on the two incomplete pairs; in the former they are in direct continuity with the stomodæal ectoderm, but it is obvious that this can not be the case with the latter. The filamental tissue on the incomplete pairs only makes its appearance some little distance below the stomodæum, and is never so strongly developed as on the other mesenteries. On these the filaments are often weak for some distance, but toward their lower termination they become greatly developed, at least on the mesenteries of the first and second developmental pairs. Here they are very conspicuous objects in sections, and developing nematocysts and gland cells in various stages can be found. The filaments have already very definite boundaries distinguishing them from the rest of the endodermal tissue.

LARVA OF ISOPHYLLIA DIPSACEA.

(Pls. XVII, XVIII, figs. 125–128.)

A colony of *Isophyllia* was collected from which larvæ were freely extruded from the beginning. On their first appearance most of the larvæ were rod-shaped, but others were pear-shaped: at first the former would crawl along the floor of the vessel in a worm-like manner, while the others would swim freely throughout the water. The larvæ were larger than those usually met with in corals, measuring fully 3 mm. in length. When first extruded they were densely opaque, and the posterior end (oral) was deeply pigmented. An hour or two after being set free some became greatly distended at the aboral pole, and as a consequence were more nearly transparent; others, again, became swollen at the oral extremity, the opposite end remaining narrow.

In the inflated larva represented in fig. 125 three pairs of mesenteries were already indicated, all extending downward from the minute, circular, oral aperture. The members of one pair of mesenteries extended nearly the whole length of the larva, and along their line of attachment were much darker and broader than the others. On one side of the pair were two other faint mesenterial attachments, which continued but a short way down the polyp, while on the other side was a third pair only just apparent, and having a still shorter vertical course. All three pairs, however, start from the uppermost extremity of the polyp.

Some of the larvæ immediately on extrusion were preserved in formol. and others in corrosive acetic, when they threw out a quantity of mucus, which resulted in the adherence of minute foreign particles. The distended larvæ nearly always collapsed during the process of preservation.

Transverse sections of the freshly extruded specimens reveal that the larvæ are practically solid bodies, the interior being filled with a compact vacuolated tissue, bearing numerous nuclei and zooxanthellæ. Boundaries in the vacuolar endoderm are indicated toward the middle, in association with the mesenteries, and in the middle of some of the larvæ there is a faint indication that the endodermal tissue is beginning to break down, but as yet they are practically solid.

Toward the oral extremity the endoderm is crowded with zooxanthellæ, which are only sparingly distributed elsewhere. An examination of the outer ectoderm reveals comparatively few algæ, and these are scattered somewhat uniformly throughout the layer. The strong pigmentation of the oral extremity, noticed among the external characters, is manifestly due to the accumulation of zooxanthellæ within the oral endoderm, not, as is more usually the case, to their presence in large numbers in the ectoderm.

Both longitudinal and transverse sections through the stomodæum indicate the absence of any actual lumen in the tube, and the compact character of the interior of the larva, above described, is not such as to suggest that the circulation of any internal nutrient fluid had been established up to the moment of liberation.

The uppermost sections through the oral extremity reveal the presence of three pairs of mesenteries, all extending from the outer wall to the stomodæum. The ventral pair, however, is represented only by the merest rudiments, and the dorsal pair extends but a short distance; neither pair stretches downward the full length of the stomodæum. The middle of the three pairs is by far the most important; its members are inserted on the stomodæum throughout its extent, and when they become free the edge is tipped with a mesenterial filament which appears as a deeply-staining tissue, wholly resembling that of the stomodæal ectoderm; the two are in absolute continuity with one another, and in every way seem one and the same tissue. The mesenterial filament extends nearly two-thirds the length of the polyp, and is very conspicuous in sections on account of the deeply-staining character of its constituent cells. The other mesenterial pairs present no indications of filaments.

I. dipsacea is of interest as showing the early stage at which the second and third pairs of mesenteries are united with the stomodæum; indeed, they seem to originate at the angle between the wall and stomodæal invagination, and thence grow down the column and the stomodæum.

The ectoderm is characterized by numerous large clear gland cells, which give out their mucus when the larvæ are preserved. Many large nematocysts are also present, and the aboral extremity displays a strongly developed nerve layer.

LARVA AND YOUNG POLYPS OF FAVIA FRAGUM.

(Pls. XIII–XV, figs. 96–116.)

The polyps of several colonies of this species collected around Port Henderson, early in April, were charged with larvæ, which were extruded singly from time to time. Occasionally, an unfertilized egg would also appear. The larvæ could be seen through the transparent walls of the expanded polyp as opaque white bodies, moving freely about in the gastro-cœlomic and tentacular cavities; upon retraction individual larvæ often remained within the tentacular cavity, distending it and forming small protuberances on the surface of the colony. The usual occurrence of the larvæ within the tentacles would indicate that they made their exit through the tips of these organs, but although large numbers escaped while the colonies were under observation the actual point of extrusion was never determined. They were either shot out suddenly, with force enough to send them some distance, or merely escaped and fell on the general surface of the parent colony.

Some of the larvæ were able to swim about immediately on extrusion; others remained motionless for a few moments either on the surface of the water or the bottom of the vessel, and then commenced vigorous gyratory movements. The rotation was clock-wise when the larvæ were viewed with the narrow oral extremity upward. When first liberated, the larvæ show considerable power of adhesion at any part of their surface; on transferring them from one vessel to another they would often fix themselves within the pipette, and require a considerable force of water to dislodge them. Specimens might adhere either by their anterior or posterior extremity for a time, and then commence moving again.

When first expelled some of the larvæ were rod-shaped bodies, about 2 mm. in length, and rounded at each end; others were pear-shaped, the broader pole being directed forward and the narrow end backward in translation; others again were oval or spherodial. The individuals, however, were able to change from one form to another. Seen with the naked eye, or by means of a lens, the larvæ were strongly opaque, an internal yellowish mass being distinguished from a colorless or slightly green external layer. The narrow, posterior, oral pole was for a long time more darkly colored than the rest of the larva.

Under the microscope also the larvæ were perfectly opaque, the ciliation was uniform, and when first extruded no oral aperture nor mesenterial divisions could be discerned. The surface appeared minutely granular, white dots being irregularly distributed over the ectoderm. The denser coloration at the narrow oral extremity was seen to be produced by an accumulation of yellow cells within the ectoderm, which gradually diminished in number away from the extremity. It was possible to determine that the coloration of the internal endoderm was also due to the presence of zooxanthellæ. Soon after liberation, extrusions of yolk granules and zooxanthellæ from the oral extremity took place, and continued from time to time (fig. 96).

Many of the larvæ underwent much alteration in shape. The oral extremity became swollen, and the aboral narrow, a reversal of the primary condition (fig. 100); but when first extruded the larvæ sometimes exhibited the swollen oral extremity and narrow aboral.

Within a day or two certain of the larvæ had settled to the sides of the vessel, becoming flattened both orally and aborally; a few zooxanthellæ were still present around the oral aperture, which had now become functional. Some specimens would again detach themselves and move slowly around. After fixation the larvæ were more transparent, and at first four pairs of mesenterial divisions were visible from the outside, and later six pairs. The settled larvæ were soon able to extend themselves, and assume the columnar form, appearing greenish in color.

The various stages of mesenterial development were quickly passed through, until all the protocnemes were present, the Edwardsian mesenteries complete and the fifth and sixth pairs incomplete. Beyond this no increase in the number of mesenteries took place during a period of three weeks. Within four days six tentacular prominences were apparent, the larvæ at this stage usually appearing flask-shaped, with a broad base (fig. 107). During the early stages the tentacles often became involved in the expanded discal tissues of which they were outgrowths, and as a consequence were indistinguishable as separate organs. In a young polyp from another batch of larvæ, the six members of the inner entocœlic cycle also appeared in advance of the members of the outer exocœlic cycle (fig. 106).

One larva was secured attached to a fragment of glass, and could thus be examined as a transparent object, and its later development observed. In seven or eight days the mesenterial filaments were visible on the first and second pairs of mesenteries as darker internal organs, and in about fourteen days six small, clear, oval areas were recognizable within the entocœle of the six pairs of protocnemes, their occurrence suggesting some connection with the first stages in the formation of the skeleton (fig. 108). They clearly correspond in position with the six septa of *Manicina* (fig. 135), and it is conceivable that they represent invaginations of the basal wall preceding the formation of the septa. No calcareous deposition however was observed to take place within them; probably the unfavorable conditions under which the larva was kept interfered with its normal development.

Small polyps are sometimes found around the larger colonies of *Favia*, and represent larvæ which have fixed themselves immediately or shortly after extrusion. From these several further stages of development have been secured, one of which is represented in fig. 109. The polyp is in a partly expanded state, and only the discal region is indicated, as seen under a low power of the microscope. The six pairs of primary mesenteries are present, the fifth and sixth pairs still free from the stomodæum; in addition to these a pair of mesenteries has appeared in each dorsal exocœle, and a small pair in each of the middle exocœles. At present the metacnemic pairs extend but a short distance over the margin of the disk, but are continued farther down the column wall. No mesenteries have yet appeared within the ventral exocœles. The significance of the stages in the mesenterial development here represented has been already noticed in discussing the appearance of the metacnemes in the Madreporaria generally.

Of the tentacles six entocœlic and six exocœlic members are already present, forming two cycles, the inner tentacles a little larger than the outer, and both slightly knobbed. In addition to these a tentacle has arisen in association with each pair of metacnemes, making sixteen in all. At this stage it was impossible from their position to say whether the new tentacles were entocœlic or exocœlic in relation to the pairs of metacnemes, but it is significant that they follow closely upon the development of the mesenteries. Most probably they are the entocœlic outgrowths which have appeared somewhat in advance of the exocœlic, following the sequence of the prototentacles.

The different stages secured in the development of *Favia fragum* afford a complete series illustrating the order of appearance of the mesenteries in corals, and it is desirable that they should be presented in their regular sequence. The series extends from larvæ with only one pair of complete mesenteries to young polyps in which fission is instituted. The earliest stage occurs in non-extruded larvæ obtained from a colony after decalcification (fig. 112). Three pairs of mesenteries are present, but only one pair is complete, and this divides the cœlenteric cavity into two unequal chambers. In the larger of these is a second pair of mesenteries, not complete as yet, but bearing rudimentary mesenterial filaments; in the smaller chamber is a third pair of mesenteries, which are very rudimentary. The first pair extends almost the whole length of the larva, the filaments strongly developed all the way; the second terminates some distance in advance of the aboral end; while the third has only a very limited course.

Larvæ which had been extruded a few hours when preserved reveal the next stage, represented in fig. 113. Two pairs of mesenteries are united with the stomodæum, and, by comparison with the previous figure, the new complete pair is evidently the dorsal pair, the second of the mesenterial sequence. The ventral pair (III, III) is no better developed than in the former figure, but in sections below the termination of the stomodæum a new pair has appeared between the dorso-lateral pair (fig. 114). This is manifestly the fourth pair in the mesenterial sequence, and it is inserted dorsal to the second pair. Also between the first and second developmental pairs are found the merest rudiments of another pair (V, V).

Sections of larvæ a little older, and in one case of a young polyp already settled, present the next stage, where three pairs of mesenteries are inserted on the stomodæum (fig. 115). Comparison with fig. 113 indicates that it is the third pair in the mesenterial sequence which has now reached completion. The fourth pair extends more upward, and the fifth pair has reached the level of the stomodæum; the sixth pair has not yet reached the stomodæal region, but is present below (fig. 116). Finally, in larvæ which have just settled (figs. 105, 106), four mesenterial pairs have become complete, and the fifth and sixth pairs are well developed in the upper part of the column, but remain free from the stomodæum.

The sequence for the protocnemic pairs is thus complete. The first and second pairs to arise become the ventro-lateral and dorso-lateral of the Edwardsian mesenteries, the third pair constitutes the ventral directives, and the fourth the dorsal directives, while the fifth and sixth pairs, incomplete as yet, arise on the ventral aspect of the second and first pairs, respectively, the fifth a little in advance of the sixth. (See diagrammatic figures on p. 508.)

A young polyp, settled on the same block of dead coral as a mature colony, affords the next stages required in the sequence—the manner of appearance of the first metacnemes. The living characters are shown in fig. 109, and a section through the decalcified polyp is diagrammatically represented on p. 509. The protocnemes are in the same stage as in the previous figure—the first four pairs are complete, but the fifth and sixth are still incomplete. Within the dorsal and middle exocœles on each side a pair of mesenteries has appeared, the dorsal pairs being better developed than the middle. In fig. 15*f*, showing the arrangement in another decalcified young polyp, six pairs of metacnemes have appeared, completing the second cycle, and all the members of the first cycle are united with the stomodæum. The six metacnemic pairs thus follow a dorso-ventral, or antero-posterior, order in their appearance, but are now practically equal and constitute the second cycle of mesenteries.

Fig. 15*g*, p. 510, shows the manner of appearance of the first pairs of mesenteries which will constitute the third cycle of twelve mesenteries, or second cycle of metacnemes, and it is at this stage that fission is introduced (p. 511).

A tangential vertical section through one of the larvæ which had settled, but in which no septal formation had yet taken place, is represented by fig. 110, and the right half of the same section, more highly magnified, is represented by fig. 111. The four complete mesenteries extend from the base to the upper wall, and present a muscular development on each face, the fibers being cut obliquely. The endoderm is still greatly thickened, especially basally, while the superficial ectoderm has undergone but little change; zooxanthellæ are altogether absent, though present in abundance in the larvæ.

A great alteration has taken place in the basal ectoderm. It is no longer a broad columnar layer, but is represented by little more than fragments, which include a few nuclei and granular matter which stains deeply. The mesoglœa is likewise extremely narrow except mesenterially, where it is much broadened. In these regions can be seen structures similar to the wedge-shaped, striated, desmoidal processes characteristic of adult polyps, so that evidently these arise at a very early stage in the fixation of the larva; hints of the same processes also appear intermesenterially, where the mesoglœa is extremely narrow. The larva from which the sections were taken had been adherent to a fragment of glass for over a week, and, though no septa were formed, it is very probable that the basal plate had already been laid down, as this is one of the first parts of the skeleton to appear. The skeletogenic ectoderm is in much the same condition as in adult polyps, in regions where growth is not proceeding rapidly.

The passage from the narrow basal ectoderm to the broad ectoderm of the column at the margin of the section is abrupt. The cells around the indented vertical part at the right extremity of fig. 111 are somewhat modified compared with those beyond, and are probably concerned in the formation of the epitheca. This is certainly the case in the slightly older polyp of *Manicina* represented in fig. 137.

YOUNG POLYPS OF MANICINA AREOLATA.

(Pl. XIX, figs. 133–137.)

To the very complete description of the early stages in the development of this species given by Dr. H. V. Wilson, in 1888, I have nothing to add, and will therefore proceed to the point at which Wilson's researches terminated, namely, the formation of the skeleton. The latest stage reached in the growth of the Bahama specimens was one in which the twelve protocnemes were present, only two pairs of which were connected with the stomodæum. The stage is comparable with that represented in fig. 134, Pl. XIX (*cf.* Wilson's fig. 39), taken from a fixed larva four days after extrusion from the parent colony.

Out of many batches of larvæ extruded from a small Jamaican colony only a few individuals became fixed, and after several days these were reduced to two, which continued to live for nearly three weeks, though under somewhat unfavorable conditions. The larvæ were attached to fragments of glass, and could be transferred from one jar to another, or submitted to microscopic examination. Usually they were kept in vessels in which living colonies of other corals, such as *Cladocora* and *Oculina*, were already established.

Shortly after fixation the first four pairs of mesenteries reached the stomodæum, but the fifth and sixth pairs remained incomplete for the whole period, and no trace of any metacnemes appeared. The tentacles protruded toward the beginning of the second week, and, at the time they could be definitely recognized, were already twelve in number.

One of the specimens, viewed as a transparent object, is represented in fig. 135. The mesoglœal portion of the mesenteries appears as a clear, colorless line; the Edwardsian mesenteries are united with the circular stomodæum, while the fifth and sixth bilateral pairs are incomplete. The knobs of the retracted tentacles stand out as darker circular patches, arranged in two alternating cycles of six each; the members of the inner cycle are entocœlic and those of the outer are exocœlic in position, varying but little in size. Within the entocœles of each of the six pairs of mesenteries is seen the first indication of the skeleton, represented by narrow, septum-like deposits, situated some distance from the periphery, and radiating toward the center. A basal granular deposit, the first formation of the basal plate, could also be distinguished, but was not studied in detail.

The second polyp is represented in fig. 136, but the corallum has not developed to the same degree as in the first polyp. In the dorsal or sulcular entocœle the calcareous deposit forms two small oval areas; in the sulcar entocœle the deposit is also oval and small; while in the lateral entocœles it bears more resemblance to a septum. The differences in extent of development suggest that the six septa may not arise with complete uniformity, but under the unfavorable conditions to which the polyps were subjected not much importance can be attached to the result. Through the oral aperture two other skeletal deposits can be distinguished, the first indications of the columella.

Fig. 135 should be compared with that given by von Koch (1897, p. 760) of the fully expanded young polyp of *Caryophyllia cyathus*. Here, also, the corallum appeared at the Edwardsian stage of mesenterial development; the tentacles are in two alternating cycles of six each, and the six primary septa have appeared, but are more peripheral in their distribution and are already united with the circular theca. In *Manicina* no thecal formation occurred during the short period the development was followed, but indications of an epitheca were observable.

Both of the young polyps of *Manicina* were decalcified, with the object of ascertaining the early stages in the modification of the polypal layers, consequent upon the formation of the skeleton.

A radial vertical section through one of the polyps, including two septal invaginations, is represented in fig. 137. It was from such sections that von Koch (1882) established the external character of the skeleton in corals. The actual outlines of the polyp are from a camera lucida drawing, while the diagrammatic outline of the skeleton has been added.

The polyp is flattened in retraction, resting upon the skeletal upgrowths, and the mouth is widely open. The right half of the section comprises a portion of a mesentery connected with the stomodæum, and bearing a mesenterial filament; the left half includes the section of a tentacle, which is only distinguishable from the rest of the ectoderm by its greater thickness and the presence of large nematocysts. The columnar and discal endoderm is narrow and contains many zooxanthellæ, while the basal, skeletotrophic endoderm is greatly thickened, except over the upper part of the septa. It is devoid of zooxanthellæ, and in its other characters closely recalls the layer as it occurs in the lower part of the skeletotrophic tissues in adult polyps (fig. 129). The mesoglœa is extremely narrow throughout.

Greatest interest attaches to the basal skeletogenic ectoderm. In the actual sections scarcely any indications of the layer remain; it has either been removed by decalcification, or, more probably, has become greatly reduced as a result of the formation of the skeleton, a condition which has been found to characterize the older regions of most coral polyps. A few nuclei occur here and there, and in places a detached mesoglœa-like membrane, representing the skeletal membrane of Bourne.

Where at each extremity the polyp turns upward the ectoderm for a short distance has undergone a similar modification, though not quite to the same degree; more of the cellular character is retained than at the base, but the passage into the broad ectoderm of the column is abrupt. It is here that the epitheca is formed, and manifestly it is nothing more than the upturned continuation of the basal plate. The epitheca and basal plate are covered only on their inner surface by the polypal tissues, while the septal upgrowths from the basal disk are clothed on both sides. The first two parts of the skeleton can therefore increase in thickness and extent only on one face; but the septa are added to on both faces. The epitheca as yet is unconnected with the peripheral septal edges, but in older polyps it rests upon their free exposed margins.

POSTLARVAL DEVELOPMENT OF SIDERASTRÆA RADIANS.

In both its free and incrusting condition *Siderastræa radians* is a very abundant coral around Jamaica, and fertile colonies have been obtained, and the development of the larvæ and young polyps followed throughout a period of seventeen weeks.

In the earliest extruded larvæ the oral aperture is already established, and the interior is nearly filled with a vacuolated, parenchymatous tissue, containing numbers of zooxanthellæ uniformly distributed throughout. Four pairs of mesenteries are present; two lateral pairs are complete, but the dorsal and ventral directives are yet free. In later larvæ the ventral directives are inserted on the stomodæum, and the fifth and sixth pairs of mesenteries have appeared. The dorsal mesenteries were complete by the time the larvæ settled, the Edwardsian stage being thus reached, but mesenterial filaments were found only on the first and second bilateral pairs of mesenteries. The ectoderm is crowded with zooxanthellæ at the oral pole, and a few occur over all the layer, but become very sparse in the older larvæ. At the aboral pole the nerve layer undergoes a strong development, and nematocysts are more plentiful than elsewhere.

Wide slits and spaces, both intermesenterially and below the stomodæum, began to appear in the larvæ shortly after extrusion, and represent the permanent gastro-cœlomic cavity. Soon the whole of the central part of the vacuolated tissue breaks down, and the middle of the cavity is occupied by a mass of organic débris, among which are zooxanthellæ and granules of various kinds. Extrusions of such débris were often observed from the free swimming larvæ. Many of the larvæ became attached to pieces of glass, and the young polyps could thus be examined under the microscope in their living condition as transparent objects, and the development of the various organs and skeleton followed step by step. The full account of the postlarval development will be published shortly, but the salient results may be here briefly summarized.

Most of the larvæ were pear-shaped, the swollen extremity as a rule being the oral or posterior end in swimming. On fixation many grouped themselves together, and thus from primarily free and independent organisms young colonies were derived. Six pairs of mesenteries—the Edwardsian members complete, and the fifth and sixth pairs incomplete—were present in the newly settled larva.

Tentacles.—Six equal tentacles, representing a primary cycle, appeared a few days after fixation; but are exceptional among all corals whose development has yet been studied in that they arise from the exocœlic chambers, not the entocœlic, as is usually the case. Two or three weeks elapsed before the entocœlic cycle began to appear, when the members developed either simultaneously or in a successive manner. They were situated central to the first cycle to arise, and for a long period remained smaller than the others. The development of the two primary cycles of tentacles was thus centripetal, the outer exotentacles appearing first and the inner entotentacles next.

The entotentacles of the adult *Siderastræa* are bifurcated toward their extremity, and in the course of their development in the larval polyps the two halves were found to appear independently, and with a period of several weeks intervening. The common peduncle was developed later, and raised the two moieties above the disk. The exotentacles remained simple throughout.

The second cycle of mesenteries having appeared, another series of tentacles protruded from the six additional exocœlic chambers, and with the primary exotentacles formed an outer cycle of twelve. Later, situated between the exocœlic cycle and the primary entotentacles, the members of the second cycle of entotentacles begin to appear, as outgrowths from the entocœles of the second cycle of mesenteries.

Thus the exotentacles, whether belonging to the primary or secondary order, appeared before the entotentacles, and from the beginning they constituted the outer cycle, at first with six and later with twelve members.

Mesenteries.—For about four weeks no increase beyond the six primary pairs of mesenteries took place, and the fifth and sixth pairs remained free from the stomodæum. Then a pair of mesenteries appeared within the dorsal exocœle on each side of the polyp. Their first indication was as two narrow lines along the column wall toward its aboral termination. These were followed by a pair in the right and left middle exocœles, and later by a pair in each ventral exocœle. For several weeks the pairs remained of different magnitudes, corresponding with the order of their appearance from the dorsal to the ventral aspect (fig. 6, p. 456). After the third month they began to extend across the disk, but, like the fifth and sixth pairs of protocnemes, never reached the stomodæum.

Corallum.—Three or four days after fixation, the skeleton was first observed in the form of six radiating septal upgrowths, practically equal in size, and situated within the six primary entocœles, about midway between the outer boundary and middle of the polyp. At the same time a narrow peripheral calcareous ring was formed, its outer surface uncovered by polypal tissues, and undoubtedly to be regarded as the *epitheca.* Macerations made later show the ring to be continuous with the *basal plate*, which very early made its appearance. A day or two after the formation of the first cycle of entosepta, the six exocœlic members began to appear, in some cases simultaneously, but in others in successive bilateral pairs from the dorsal to the ventral aspects (fig. 12, p. 492).

During the course of the third week other calcareous deposits took place, some appearing as angulated continuations of the primary septa, and others arising wholly independent. For two or three months the further development consisted mainly in the increase in size and complexity of the parts mentioned, the general impression being that of two cycles of septa, a larger and a smaller, having their peripheral extremity enlarged in a Y-shaped manner, but free from the epitheca. The columella was formed partly from independent upgrowths from the basal plate, and partly by centripetal extensions of the entosepta.

On the establishment of the second cycle of mesenteries, which naturally corresponded in position with the primary exosepta, new calcareous formations appeared independently at the periphery of the entocœles, and later fused with the primary exosepta already in the same radius. The peripheral angulations of the primary exosepta became new and independent exosepta, situated within the twelve exocœles. The skeletal changes now going on were somewhat obscure and complicated, but according to my interpretation they afford clear evidence that the members of the second cycle of entosepta must be regarded as new formations, even though later they fuse with the remnants of the primary exosepta. The continuations of the primary exosepta remain exosepta, and for the time being constituted the third cycle of septa. A distinct dorso-ventrality was manifest in the development of the septa.